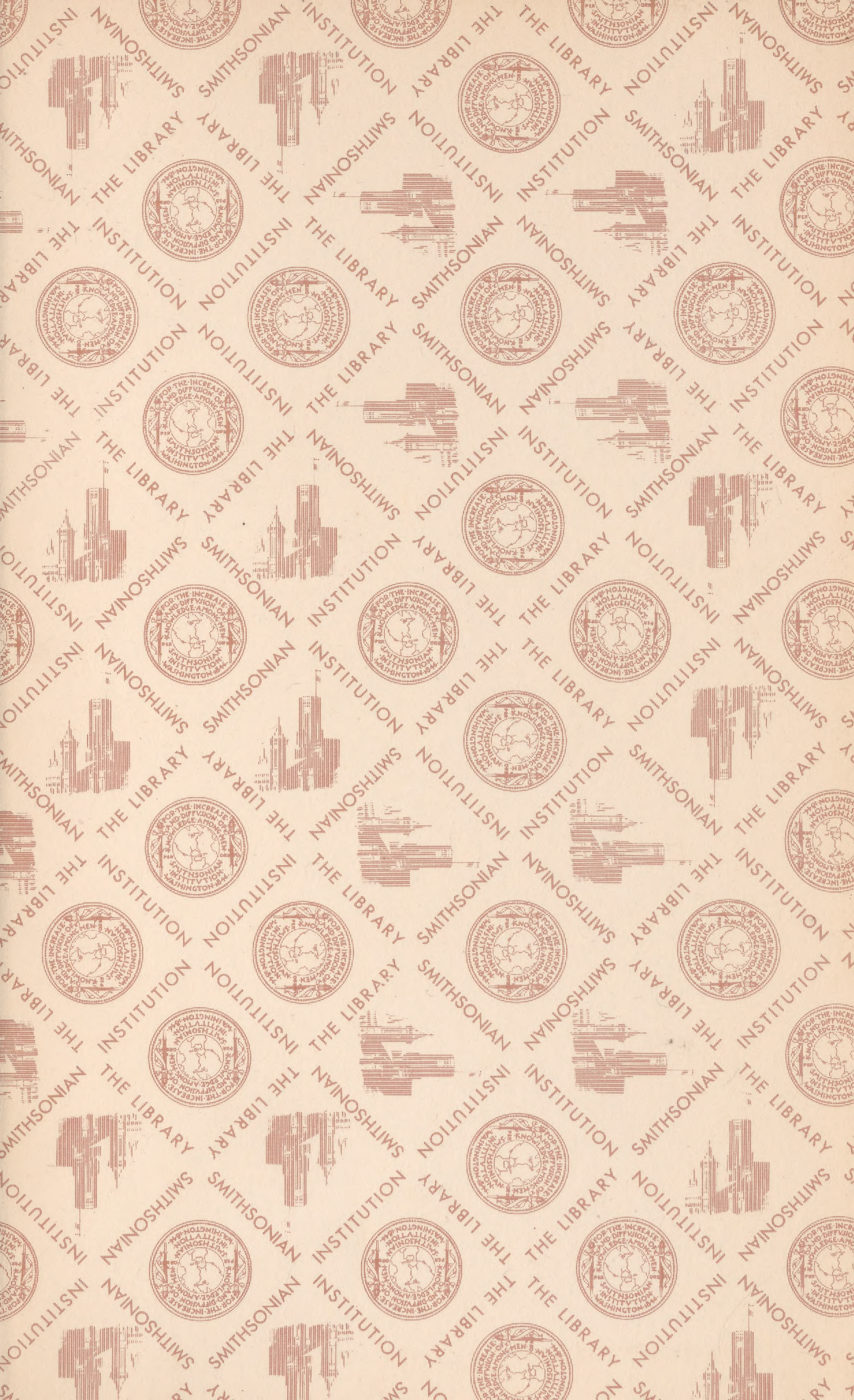
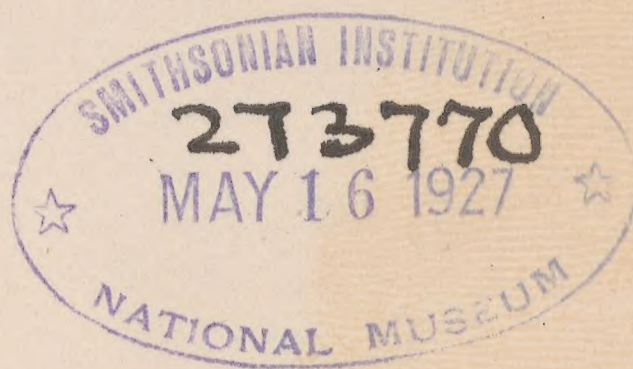
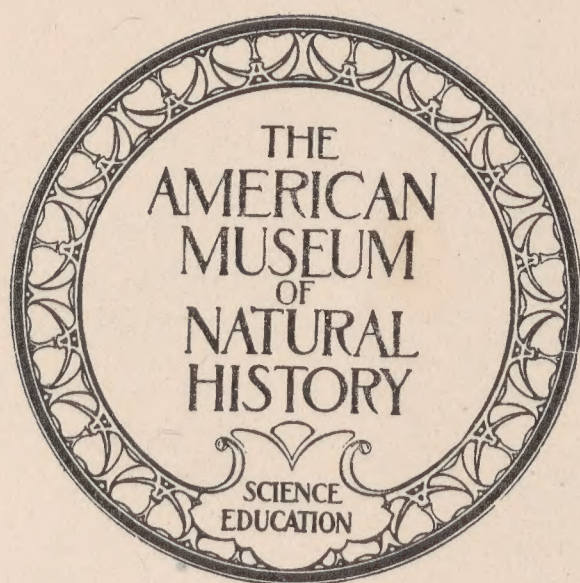






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ERRATA

- Page 9, line 21 from top, for time time read same time.
- “ 23, No. 12816 in ms. incorrect, number not ascertainable.
- “ 82, line 19 from bottom, for *Parameles* read *Perameles*.
- “ 83, line 14 from bottom, for No. 6346 read 6364.
- “ 90, Fig. 17, for No. 2702 read 2072.
- “ 138, Fig. 4, for Compare with Plate I, Fig. 10, read Compare with Plate I, Fig. 8.
- “ 138, Fig. 4, for Compare with Plate I, Fig, 11, read Compare with Plate I, Fig. 9.
- “ 328, Fig. 4, for teeth read tooth.
- “ 391, middle of second line, for maxillary read premaxillary.

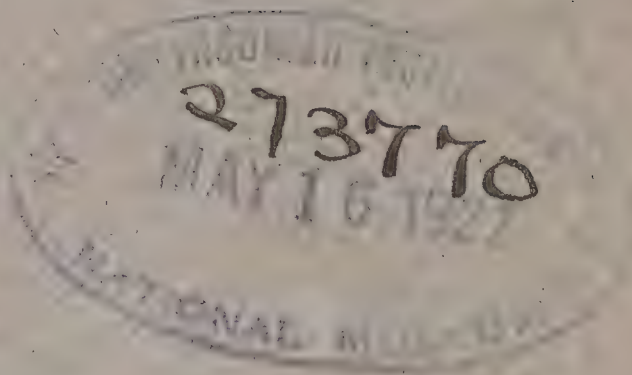
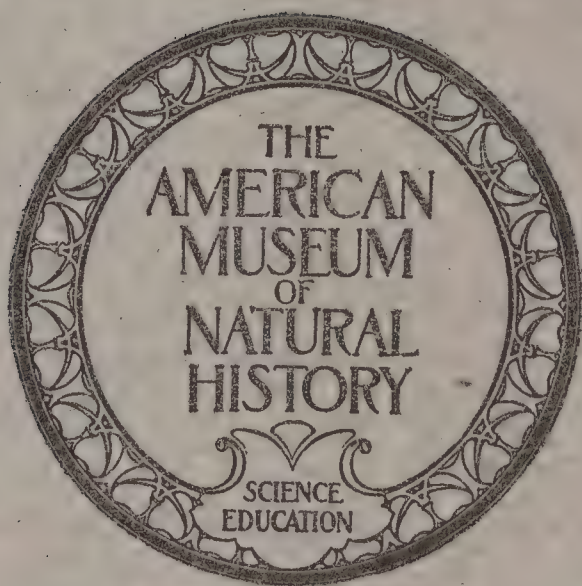
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BULLETIN
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OF NATURAL HISTORY**

VOLUME LI, 1924-1925

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BULLETIN
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VOLUME LI, 1924

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Article I.—MIOCENE OREODONTS IN THE AMERICAN
MUSEUM

By F. B. LOOMIS

As a result of a series of expeditions undertaken annually since 1905, the American Museum has accumulated a large collection of mammals from the various beds of the Miocene, especially in the region of western Nebraska and South Dakota. Parts of this collection have already been described, but the oreodonts have remained almost unknown. This group, by the generosity of Prof. H. F. Osborn and Dr. W. D. Matthew, it has been my privilege to study; and I here thank Dr. Matthew for the many suggestions which have aided me in the study of the group. The collections from the lower and upper Rosebud beds are particularly full, and rich in forms which help toward an understanding of the Oreodontidae,—a group none too easy to understand, because it contains such a large number of genera and species and, at the same time, displays so little variation in the dentition and foot structure, this in spite of the fact that there were wide ranges of adaptation in the group.

The study of this group involved a comparison of the material with the collections in the Carnegie, National, Princeton, Yale and Amherst Museums, in order to find a better basis, or bases, for the distinctions between genera and species. This led to a review of various parts of the skull in the hope of finding features which could be followed through the various genera and would serve as criteria for distinguishing one from the other and would at the same time register relationships. Two regions have proved of primary value in tracing the relations of the various genera to one another: first, the premolar dentition; and second, the rear of the skull, including the otic region. Whether dealing with such short-headed types as *Merychys* and *Leptauchenia* or with long-headed genera like *Promerycochærus*, the dental formula remains the same and

the character of the molars varies but little; but the premolars do vary, and considerably, also purposefully; so that by their aid generic distinctions and relationships may be clearly traced. Not only is this true for the Oreodontidæ; but these premolars are equally important in distinguishing the phyla of artiodactyls and, while I have not carried this study through all the genera of the other phyla of artiodactyls, so far as I have gone it is equally useful in those other phyla outside the Oreodontidæ.

Inasmuch as the premolars of artiodactyls have not been studied systematically and there is no standardization of their changes, it will be necessary to take a little space to discuss premolars in general and to describe certain structures which may be referred to more conveniently in the future, if given names.

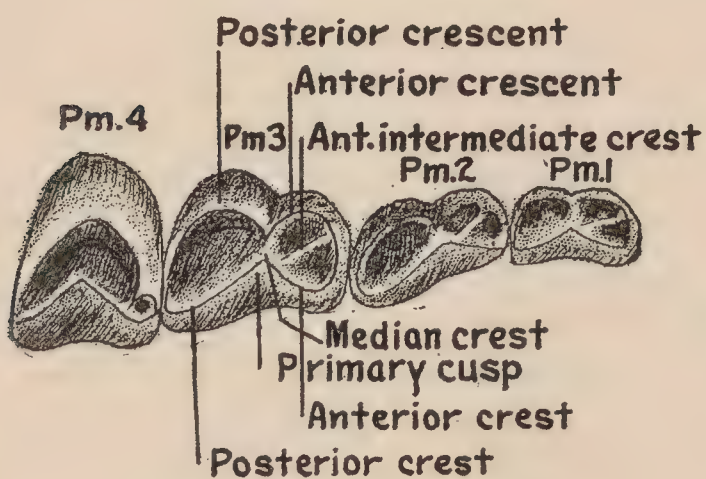


Fig. 1. Upper premolars, left side of *Merycoidodon culbertsoni* Leidy. Natural size.

The upper premolars of *Merycoidodon culbertsoni* may serve as primitive enough to illustrate early characters and, at the same time, as specialized enough to illustrate the features of the whole group. We may start with premolar 1, the least modified of the series. It consists of a primary cusp (the protocone?) on the outer side of the tooth. From the primary cusp there extends forward a crest which I would designate the

ANTERIOR CREST, and a second crest extends to the rear, the POSTERIOR CREST. From the primary cusp a slight ridge runs to the middle of the inside of the tooth, and I would call this the MEDIAN CREST. These three crests will appear on all the premolars. Those farther to the rear, like premolar 3 or 4, may have other crests, quite generally one running from the primary cusp to the middle of the anterior root of the tooth, and this I would call the ANTERIOR INTERMEDIATE CREST. In like manner, a weaker crest may extend from the primary cusp to, or toward, the middle of the posterior root of the tooth, and this is the POSTERIOR INTERMEDIATE CREST. Lastly, above both the anterior and posterior roots, on the inner side of the tooth, there may be a fold, either low or extending to the full height of the tooth. These I have designated the ANTERIOR and POSTERIOR CRESCENTS. One or both may be either fully developed or entirely lacking. This nomenclature is illustrated in figure 1.

These crests and crescents may all appear on one tooth and are best developed on the third upper premolar. The marked development or

suppression of certain crests, or crescents, is characteristic of phyla and genera. In some cases a further modification is present in the development of a cusp-like pillar at the junction of the median crest and the posterior crescent. The fourth upper premolar appears like a half-molar, and this peculiarity is attained differently in different phyla, making this tooth and its origin of prime importance in studying artiodactyls. A few cases will illustrate this.

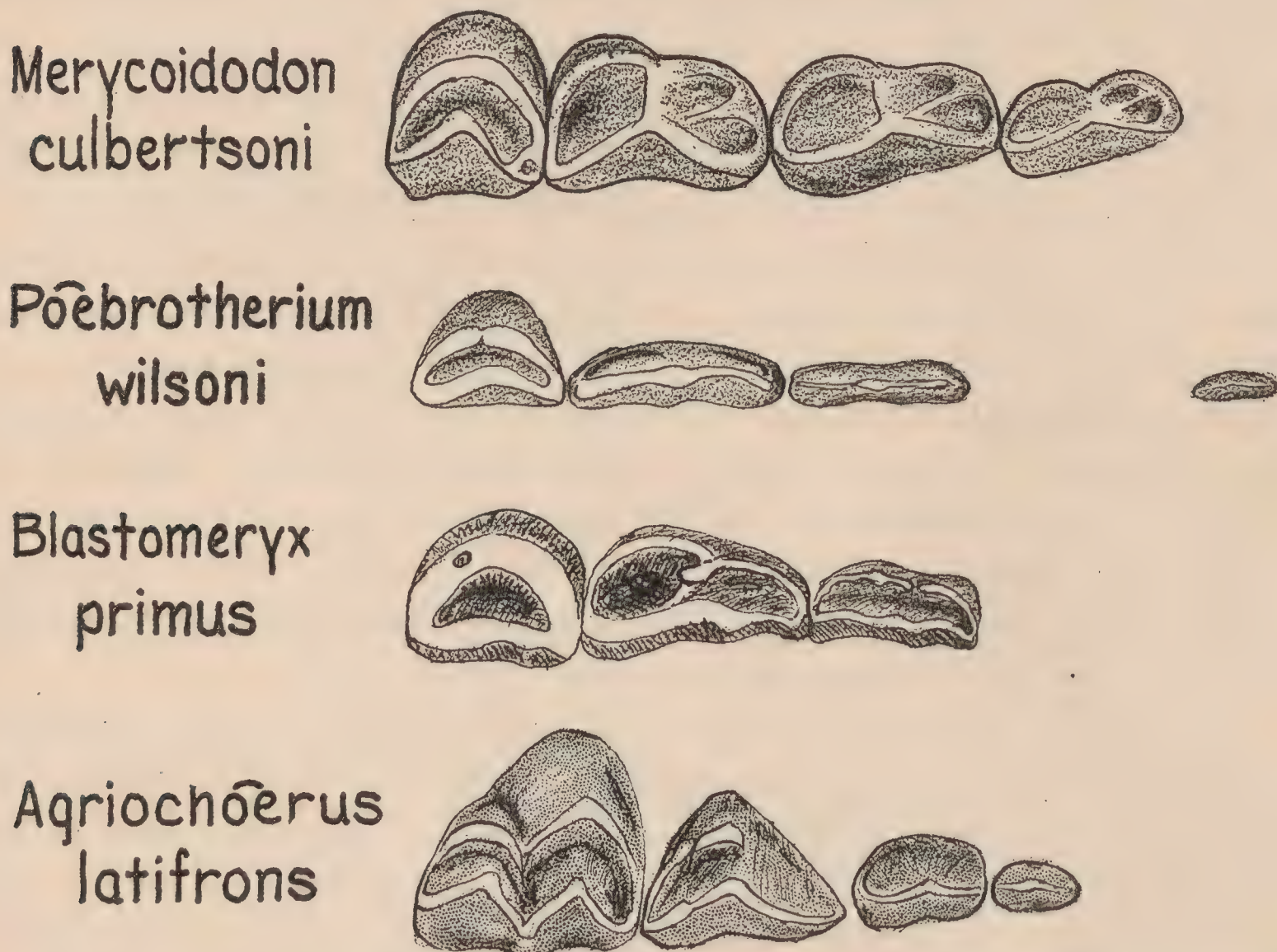


Fig. 2. Upper premolars, left side, of an oreodont, a camel, a deer and an agriochœrid, to show differences in character and mode of development.

In the oreodonts, examining the premolars from the first to the fourth, it will be seen that premolar 4 corresponds to the posterior half of premolar 3, the posterior crescent being greatly developed and united to the median crest, and all trace of the anterior part of the tooth has disappeared, except for a tiny pit in the anterior outer corner, which is the vestige of the outer part of the anterior basin seen on premolar 3. In a few very primitive genera, traces of both parts of the anterior basin are retained; and in the more advanced genera, all trace of the anterior half of the tooth is lost. See figure 4.

In contrast with this, the fourth premolar of camels is formed by shortening the whole of premolar 3; its inner crescent is composed of

both the anterior and the posterior crescents united, and there is never any pit in the corner. Then the other premolars are characterized by the narrowness and lack of intermediate crests. The fourth premolar of the deer is developed in still another manner. As in camels, both anterior and posterior crescents are developed, together with anterior, median and posterior crests, but the intermediate crests are wanting. Also as in camels, premolar 4 is formed by the shortening of the anterior-posterior diameter of such a tooth as premolar 3; but, in this case, the posterior crescent overlaps the anterior crescent to a greater or less extent. In some cases, between the overlap a pit is preserved, which is located on the inner side and just behind the middle of the tooth. This is more marked in the advanced genera. The *Agriochoeridæ* differ widely from the other artiodactyls, first, in that the anterior portion of each premolar is simple, without either crests or crescents, while the posterior portion has strong crests and a strong crescent. The fourth premolar is unique among artiodactyls, so far as I have seen, in being molariform in character, with two outer cusps and two inner cusps. Then too this double character is attained in an unexpected manner, for the whole tooth is developed from the posterior portion of premolar 3, the outer cusps being formed by dividing the posterior crest, and both inner cusps being already indicated on the rear half of the posterior crescent of premolar 3.

Among the artiodactyls, the lower premolars also have certain fundamental characters in common. As in the upper premolars, there is the primary cusp on the outer side, and from it a crest to the front, the ANTERIOR CREST, and another to the rear, the POSTERIOR CREST. A MEDIAN CREST is usually developed, and both ANTERIOR and POSTERIOR INTERMEDIATE CRESTS may be present, though one or the other of these last two may be lacking. ANTERIOR and POSTERIOR CRESCENTS are usually indicated on premolars 1 and 2; and may be more, or less, fully developed on premolars 3 and 4. A cusp-like pillar is likely to develop at the junction of the median crest and the posterior crescent, and in some cases the middle of the posterior crescent is developed to appear almost like a cusp. Premolar 1 is modified into a caniniform tooth in both form and function. Premolar 4 is not modified to molariform character, except in *Agriochoeridæ*, so that the change from premolar to molar teeth is abrupt. Premolars 3 and 4 are the most typical teeth in this series.

Among the oreodonts, the anterior, median and posterior crests are well developed, and the posterior crescent is strong; but the anterior and posterior intermediate crests are usually weak or lacking. Both crescents are likely to be indicated on premolar 2, but usually only the

posterior crescent is well developed on premolars 3 and 4. Camels have the lower premolars markedly compressed, and only one basin, which is a narrow one on the posterior half of premolar 4, between the posterior crest and crescent. Deer have complex lower premolars, on which the anterior, median, posterior intermediate and posterior crests are well developed; but the inner side does not develop the crescents to any large extent, so that basins are not inclosed between the crests. Agriochoeridæ are again peculiar in the structure of their lower premolars, especially the

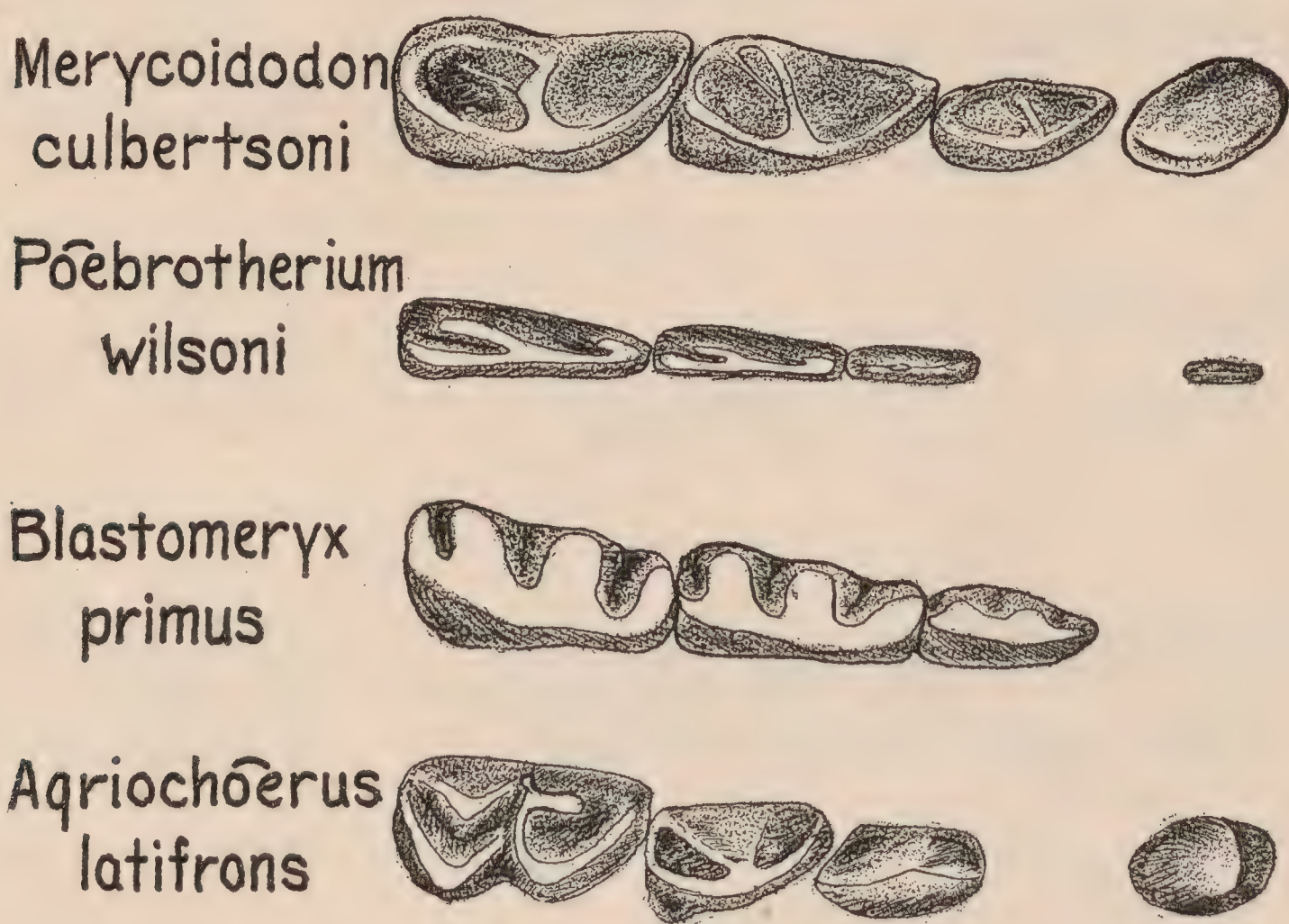


Fig. 3. Lower premolars, right side, of an oreodont, a camel, a deer and an agriochoerid, to show differences in character and mode of development.

fourth, on which the posterior portion is more or less independent. The anterior crest is strong, but the anterior crescent is shortened into a pillar-like cusp, unique. The posterior crest also is short and independent, making a cusp, and the posterior crescent also is shortened and tends to become an independent cusp.

Turning to the phylum Oreodontidæ, we may consider the various genera to find generic variations and phyletic relationships, which, in the discussion of the genera, are correlated with the characters of the body and especially with those of the rear of the skull which are shown in figures 9 to 26.

In the Uinta beds there are several selenodont artiodactyls which from time to time have been suggested as related to the higher oreodonts.

Studying the premolar dentitions of these, however, such genera as *Eomeryx* and *Protagriochærus* seem to belong to the oreodont phylum but by no means in the ancestral line, in fact far to one side, having developed a dentition which is specialized, though the shape of the skull, especially the orbit's being open behind, is primitive. In like manner, *Protoreodon* is in the oreodont phylum; but in this case, we have a form which is much nearer to the ancestral line, though not directly in it.

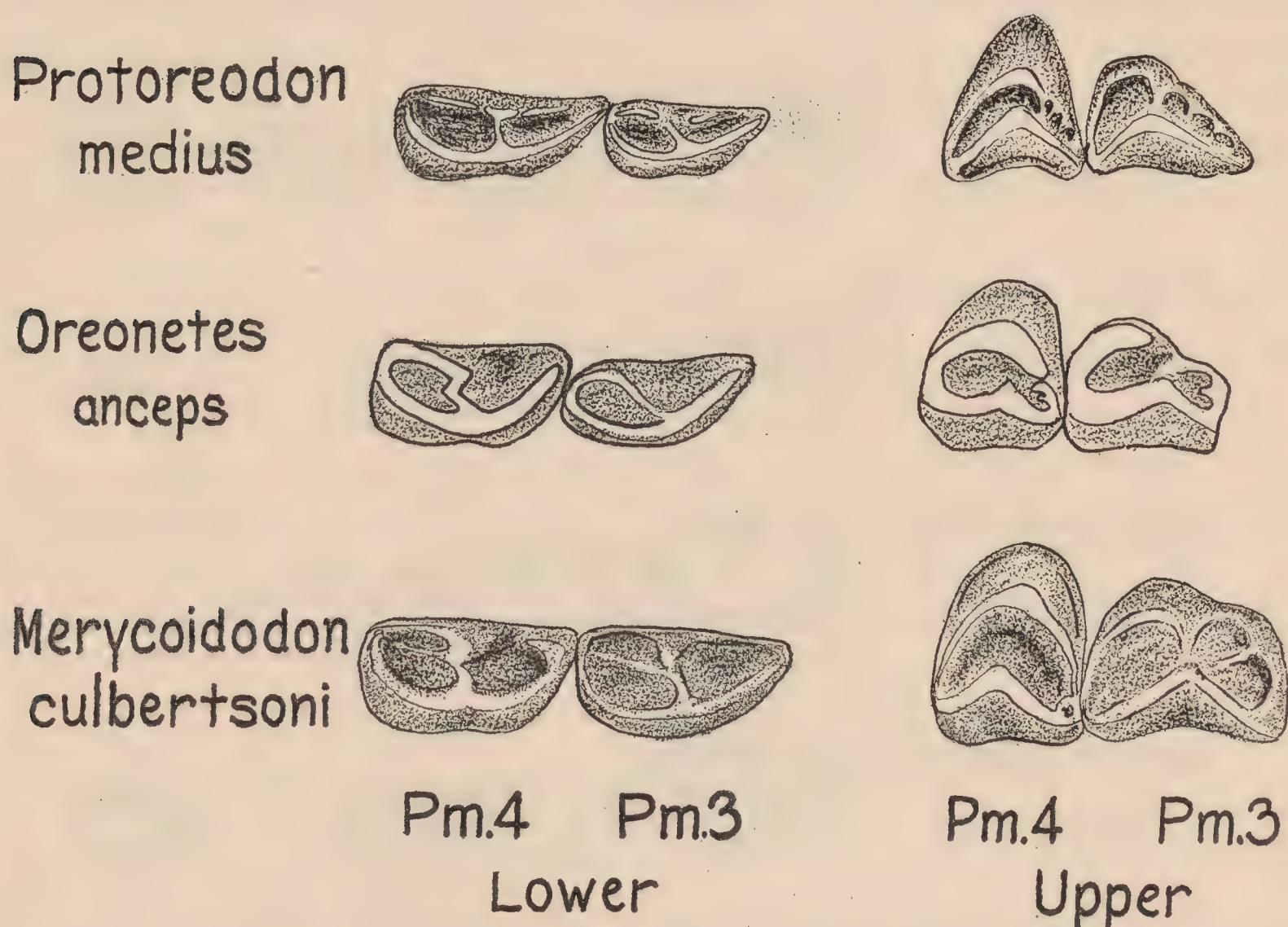


Fig. 4. The third and fourth premolars of oreodonts, uppers from the left side, lowers from the right side, to show the development of the *Merycoidodon* line.

All the above forms have the tiny bulla which is characteristic of *Merycoidodon* and which separates this group of oreodonts from the much larger group with large bullæ.

Three genera are closely related and make up the series which is characterized by the tiny bulla, *Protoreodon* of the Uinta, *Oreonetes* of the Titanotheres beds and *Merycoidodon* of the middle Oligocene. The third and fourth upper and lower premolars are shown in figure 4 for comparison. In *Protoreodon*, upper premolar 3 has, besides the anterior and posterior crests, a weak median crest, no posterior intermediate crest, but on the front portion of the tooth, two weak anterior intermediates. The same features are repeated on the fourth upper premolar, which, in

this case, has progressed toward the half-molar type less than in any other genus. On the lower premolars, the anterior, median and posterior crests are well developed, and both crescents are clearly marked, though low. These characters indicate nearness to the ancestral type, but the anterior crescent on the lower premolars suggests a position to one side of the main line, as does also the rather elongate type of the feet.

*Oreonetes*¹ has the upper third premolar with a weak median and anterior intermediate crest. In this genus the posterior crescent is well developed. The fourth premolar is formed typically by the reduction of the front half of the tooth, but in this case traces of both parts of the anterior basin are still preserved on this tooth. On the lower premolars the anterior crescent is wanting and the posterior crescent is united to the median crest, making a well bounded and typical posterior basin.

Merycoidodon has rather broad premolars on which the anterior portion of the tooth is less developed than usual. Premolar 3 has the anterior intermediate crescent well developed, dividing the basin into two equal parts. Premolar 4 is formed in the usual way, but in this case, in teeth not too much worn, there is a pit in the anterior external corner representing the outer portion of the anterior basin. On the lower premolars, the anterior intermediate crest is lacking and the posterior intermediate crest, while present, is weak and has a peculiar position, in that it comes off from the median crest instead of the primary cusp.

Turning to the group of oreodonts marked by the presence of very large bullæ, *Limnenetes* from the Titanotheres beds, *Eporeodon* from the Middle and Upper Oligocene (perhaps into the Miocene) and *Mesoreodon* of the Lower Miocene form a group which have much in common: in medium length and weight of limbs; in having the back of the skull compressed and drawn out to the rear, and also in the character of their dentition. All tend to have the median cusp weak and at the same time the crescents, especially the posterior crescent, well developed. This is even more true of the later representatives of this phylum.

The type of *Limnenetes* is very old and the pattern of the teeth has to be taken from associated material, on which only the upper premolars have good dentitions. In this form, though the skull has the orbit open behind and is in every way primitive, the upper teeth are enough specialized to cause the genus to be regarded as a little to one side of the main phyletic line. On premolar 3 the anterior crescent is barely indicated and the intermediate crests are wanting. Premolar 4 has the posterior

¹The name is one given to Douglass's *Limnenetes? anceps* in an article to appear in the Annals of the Carnegie Museum.

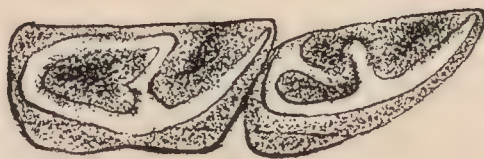
Limnenetes
platyceps



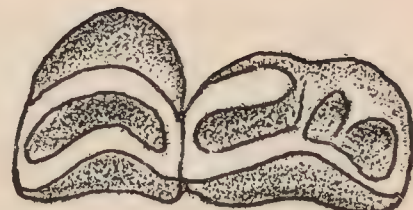
Eporeodon
dickinsonensis



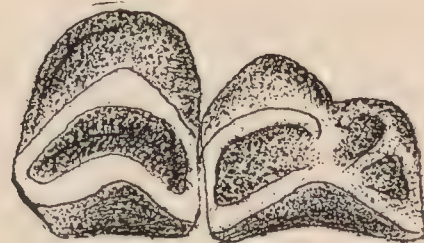
Mesoreodon
megalodon



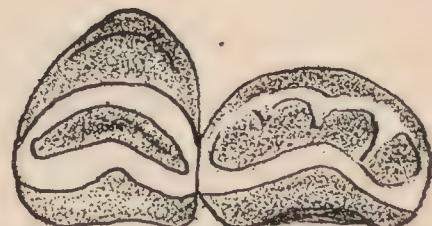
Promerycochoerus
grandis



Merycochoerus
magnus



Pronomotherium
altiramum



Pm.4 Pm.3

Lower

Pm.4 Pm.3

Upper

Fig. 5. The third and fourth premolars of oreodonts, uppers from the left side, lowers from the right side, to show the development of the *Merycochaerus* line.

crescent fully united to the median crest and no trace of a pit in the anterior external corner, as might be expected in so early a form. *Eporeodon* has the third premolar with the anterior portion more nearly equal in size to the posterior portion than is general in this group. The anterior intermediate crest is well developed and both crescents are well marked. Premolar 4 forms in the normal manner by the reduction of the anterior half. In the case illustrated, *E. dickinsonensis*, an early species, traces of both parts of the anterior basin are preserved, but in the Upper Oligocene and John Day species only one pit is present in this position. The third lower premolar has strong anterior, median and posterior crests, but very weak crescents or none. The posterior basin is divided by a ridge running back from the median crest, which is typical. Premolar 4 has no trace of this ridge, but has the posterior basin completely inclosed between the posterior crescent and the posterior and median crests. It shows also a considerable tendency for the development of a pillar-like cusp at the junction of the posterior crest and the median crest; and this enlargement is prolonged forward noticeably, a feature more developed in some of the later genera.

Mesoreodon was founded on *M. chelonyx*, which is related to *M. megalodon*. Both of these have skulls tending to the same form as that characteristic of *Promerycochærus*, but at the time they have a skeleton which is about like that of *Eporeodon* or *Merycoidodon*; so I take this to represent a group which was transitional between *Eporeodon* and *Promerycochærus*, though the known representatives of the genus are contemporaneous with these genera. The other species which have been referred to *Mesoreodon*, such as *M. longiceps* and *M. laticeps*, are far from the type species and close to the form which Douglass called *Merycoides*; so that I should group them with *Merycoides cursor* as a separate line. In the true *Mesoreodon*, the front half of the upper third premolar is shortened, and the anterior intermediate crest, though small, is well developed. The posterior crescent incloses a basin on the rear of the tooth. On the anterior external corner of premolar 4 there is a pit in *M. chelonyx*, but none in *M. megalodon*. In like manner, the lower premolars are intermediate. The genus is distinguished in that on premolar 3 only the rear portion of the posterior crescent is developed, and that is united with the posterior intermediate crest. On premolar 4 the intermediate crests are wanting, but the posterior crescent is well developed and confluent with the pillar-like cusp which is developed at the junction of this crescent with the median crest. This pillar-like cusp is not so prolonged forward as that of *Eporeodon*, but is more distinct. Neither is it as isolated as in *Promerycochærus*.

In the Miocene we find three large oreodonts which have in common very short limbs, heavy bodies and skulls with wide-spreading arches. *Promerycochærus* of the John Day and Lower Miocene has a prolonged snout and nasal bones, while *Merycochærus* has the head shortened and the nasals retreating far back on the skull, and *Pronomotherium* has the shortening of the nasal region in such exaggerated degree that the nasal bones end as far back as the eyes. These forms are successive in time and would seem to be a progressive series, but in each case the one genus abruptly disappears and is replaced by the later genus without intermediate forms. The dentition, however, shows that they are of common stock, but that one genus is not derived directly from its predecessor.

The *Promerycochærus* upper premolars have both the anterior and posterior crescents well developed, but the median crest is weak, hence there is a suggestion of the union of the anterior and posterior basins. The anterior basin is partly divided by a weak anterior intermediate crest. The fourth premolar has entirely lost the pit in the anterior external corner. The lower premolars are narrow and compressed. The third lower premolar has no anterior crescent and only a weak posterior one. The posterior intermediate crest is well developed, and it completely divides the posterior basin. Premolar 4 is entirely characteristic, in that the pillar-like cusp at the junction of the posterior crescent and the median crest is greatly enlarged; and not only that, but it remains distinct from both the crescent and the crest until the tooth is worn far down. Furthermore, there is developed on the posterior crest an enlargement which appears like a smaller cusp. This tooth, therefore, is entirely distinctive, and, because *Desmatochrys* corresponds entirely with this dentition, I regard it as a small, though not the smallest, *Promerycochærus*.

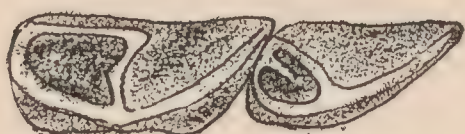
Merycochærus has no pit in the anterior external corner of premolar 4. The other upper premolars have the crescents both well developed and the median crest rather weak. The lower premolars are compressed and narrow. Premolar 3 has lost the intermediate crests, its anterior portion being simple and the rear inclosing a simple basin. Premolar 4 is the characteristic tooth, having the posterior crest and crescent inclosing a simple basin, but at the junction of the median crest and the posterior crescent, the pillar-like cusp is not distinct, but is prolonged far forward, into the anterior basin. This, though related to the condition of the corresponding tooth in *Promerycochærus*, can not be derived from it but seems rather to indicate independent development from common ancestry.

Pronomotherium has a very peculiarly shaped skull, but its dentition is by no means so highly specialized. Upper premolar 3 has so weak a median crest that anterior and posterior basins are confluent, especially as both are bounded by well-developed crescents. There are traces of the intermediate crests, but they are small. The third lower premolar has the anterior portion of the tooth prolonged. The anterior crescent is present,

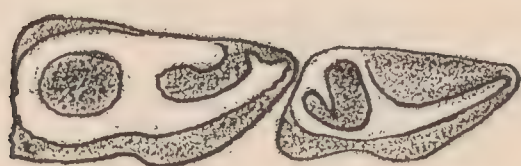
Merycoides
longiceps



Phenacocoelus
typus



Ticholeptus
petersoni



Metoreodon
relictus



Pm.4 Pm.3
Lower

Pm.4 Pm.3
Upper

Fig. 6. The third and fourth premolars of oreodonts, uppers from the left side, lowers from the right side, to show the development of the *Ticholeptus* line.

but weak; the median crest is well developed, but there are no intermediate crests. Premolar 4 has a strong median crest, with a cusp-like pillar at the junction of this crest and the posterior crescent, which projects forward as in *Promerychochærus*, but is not isolated as in that genus. Such teeth as these can scarcely be derived from those of *Merychochærus*, and it will be necessary to go back pretty well in the Miocene to find the form which would be the common ancestor of these two genera.

Merycoides, *Phenacocælus*, *Ticholeptus* and *Metoreodon* are a group of genera, all of which have the medium type of limbs, neither long nor short, light nor heavy; skulls which are lightly built, with light arches, and the supra-occipital crests not prolonged behind. In the rear of the skull there are usually pits in the exoccipital bones, and in many species there is a marked tendency to vacuities in the antorbital region. The type of the genus *Merycoides* is *M. cursor*, and I should associate with this such species as have been known as *Mesoreodon longiceps* and *Mesoreodon laticeps*. In all these genera the anterior portion of the upper premolars is shortened, the median crest is weak, and the posterior crescent, though swollen, does not unite with the median crest. In the lower premolars the anterior intermediate crest and the anterior crescent are lacking or weak. The posterior portion of premolar 3 is always inclosed by the median crest, posterior crescent and posterior crest, and into this basin the posterior intermediate crest projects from the rear. Premolar 4 has the rear portion of the tooth inclosed like that of premolar 3, but there is no posterior intermediate crest. There is a marked tendency for the pillar-like cusp to be developed and to project far forward into the anterior basin.

Merycoides does not show specialization in any line and the description just given for the whole group will answer for this genus.

Phenacocælus is a genus in which the skeleton is not specialized, but the skull is highly modified. Its general character is that of *Merycoides*, but there are excessively deep pits in the rear of the occipital bones, two small vacuities in the frontal bones and large vacuities in the antorbital region. The teeth are those of *Merycoides*, except that they are less advanced, so that this form belongs to the *Ticholeptus* line but had already begun to develop its peculiarities before the lower Miocene, when we are first acquainted with it.

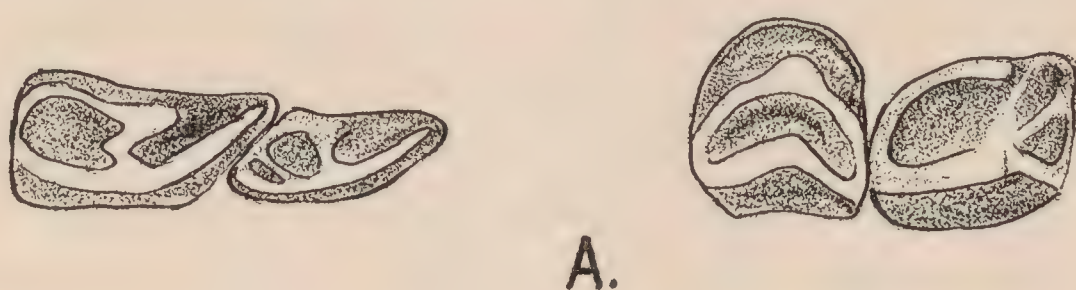
Ticholeptus is a large group of Miocene to lowest Pliocene oreodonts which show a tendency to shorten the skull and develop large vacuities in the antorbital region. The teeth are similar in plan to *Merycoides*, but more advanced, first, in a greater shortening of the anterior portion of premolars 1 to 3 of the upper jaw, so that the anterior basin is in many cases so shallow as to appear almost flat, and, second, in the greater thickening of the posterior crescent of premolar 3. In the lower dentition, premolar 4 has the anterior end of the anterior crescent bifurcated, which serves easily to identify this genus or the following one.

Metoreodon is a Pliocene genus based on lower jaws and is an exaggerated *Ticholeptus*. It is distinct in that the teeth are hypsodont;

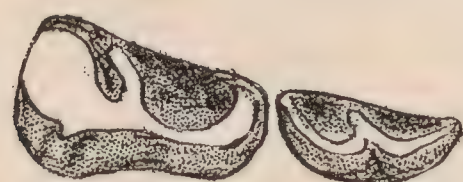
premolar 3 has the anterior crescent developed into an inner boundary of the anterior basin, and the posterior basin is divided completely by the posterior intermediate crest in a peculiar position parallel to the median crest. Premolar 4 is also distinctive in the small size of the posterior region, and the great enlargement of the pillar-like cusp which almost fills the anterior basin.

Merychys is a genus about which there has been endless confusion. It was based on *M. elegans*, and to this genus were referred a large number of species which have proved to be of entirely different character. In addition, the genus is extremely conservative, and such a species as *M. elegans* has been identified as occurring in horizons all the way from Lower

Merychys
minimus



Leptauchenia
decora



B.



Pm.4

Pm.3

Pm.4

Pm.3

Lower

Upper

Fig. 7. Third and fourth premolars of oreodonts, uppers from the left side, lowers from the right side, to show the development of *Merychys* and *Leptauchenia*.

Miocene to Pliocene, to which horizon the type belongs. On page 31 I have listed the species which truly belong to this genus. *Merychys* had light slender limbs, a short, rather wide skull, not prolonged behind, and with pits in the exoccipital bones, usually a small antorbital vacuity, but this last is variable. The teeth of the upper jaw are shortened. This is accomplished in the premolar series by the reduction of the anterior portion. The illustration (Fig. 7A) shows about an average amount of shortening of this anterior region. In the lower Rosebud species *M. curtus*, the anterior is less shortened, and in the Pliocene species *M. elegans*, it is much greater. The lower premolars remind one of *Merycoides*, but the posterior crescent is not so much developed. This genus

runs from the lowest Miocene into the Pliocene, with very little change in character, and is represented in the John Day by *Oreodontoides oregonensis*, which I take to be a *Merychys* slightly less advanced than the eastern representatives. *Paroreodon* is another John Day genus which belongs close to *Merychys*, but is different in the greater depth of the skull and in the peculiar pointed, large bullæ.

Leptauchenia and *Cyclopidius* represent a line of oreodonts which appears suddenly in late Oligocene times and disappears as suddenly at the end of the Deep River epoch. The skeleton is lightly built and slender, somewhat like *Merychys*, except that there are five toes on the front foot. The skull is excessively shortened; there are enormous bullæ and great vacuities in the antorbital region. This phylum probably unites with the light-limbed *Limnenetes* of the Lower Titanotheres beds, though I doubt if this genus is the actual ancestor. There is much in common between this line and *Merychys*, and these two lines probably come together in lower Oligocene times. The upper premolars of *Leptauchenia* seldom show their pattern, since they are hypsodont and almost always badly worn. When, however, little-worn teeth are studied, it is seen that the upper premolars are shortened by the almost complete suppression of the anterior portion. When such teeth are worn, the median crest appears like the anterior crest, and the tooth seems to stand transversely in the jaw. This peculiar appearance, however, is due to the suppression of the anterior basin. Premolar 3, as seen in figure 7B, has a large posterior crescent which does not unite with the median crest. Premolar 4 in little-worn teeth shows the pit in the anterior external corner. The lower premolars are characterized by the entire lack of crescents and intermediate crests. The fourth premolar is unique in the enormous swelling of the posterior crest, so that this fills the posterior basin. *Cyclopidius* is *Leptauchenia* exaggerated, with the incisors reduced to two on either side of each jaw. *Chelonocephalus* is a *Cyclopidius* with a markedly depressed skull.

Five lines of Oreodontidæ have been recognized in the foregoing. First, there is the fundamental division based on the tiny or large bulla, and a line ending in *Merycoidodon* represents the tiny bulla. Second, the main line of medium-heavy forms with large bullæ leads into the short-limbed, heavy-bodied *Pronomotherium* and *Promerycochærus* type. Third, there is another group leading from the intermediate stock of the Middle Oligocene to *Ticholeptus* and *Metoreodon*. Fourth, *Merychys* is a very conservative line of lightly built small forms, the Oligocene representatives of which are unknown. Fifth, the extremely light-limbed and

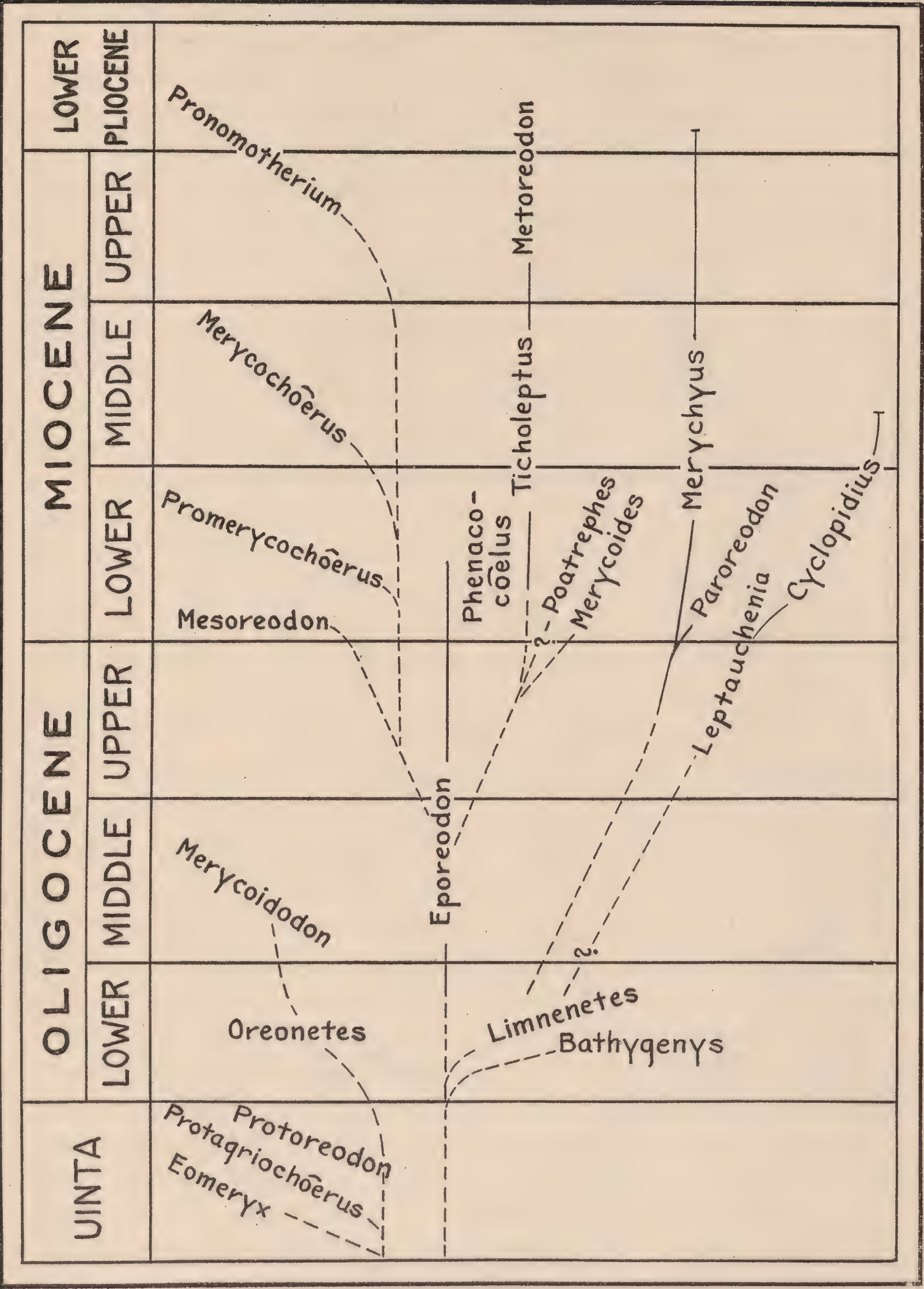


Fig. 8. Phylogeny and Geological Sequence of the Oreodonts.

short-headed *Leptauchenia* and *Cyclopidius* represent some special adaptation which it is very difficult to interpret.

Throughout the whole group there is great uniformity in the character of the dentition and the feet. There is none of the progressive adaptation and change characteristic of the grazing types, and I feel that this is probably due to a constancy in the type of food and feeding-ground. I should take the food to be leaves, seeds and fruit; and the feeding-ground the more or less wooded valleys along the streams. One feature characteristic of the group tends to confirm this, and that is the distinctness of the faunas from the different localities. The genera are widely distributed, but the species are local. It would seem that of the various river valleys each had its group of oreodonts, and, when there was a change in climate or other living conditions, the fauna of any given valley was either exterminated or replaced by a new immigration.

The various genera are compared in the chart on the following pages, and their relationships expressed as nearly as I can see them in the phylogenetic tree on page 15.

The following pages describe the new material of the Miocene belonging to the Oreodontidæ and in The American Museum of Natural History.

PROMERYCOCHÆRUS

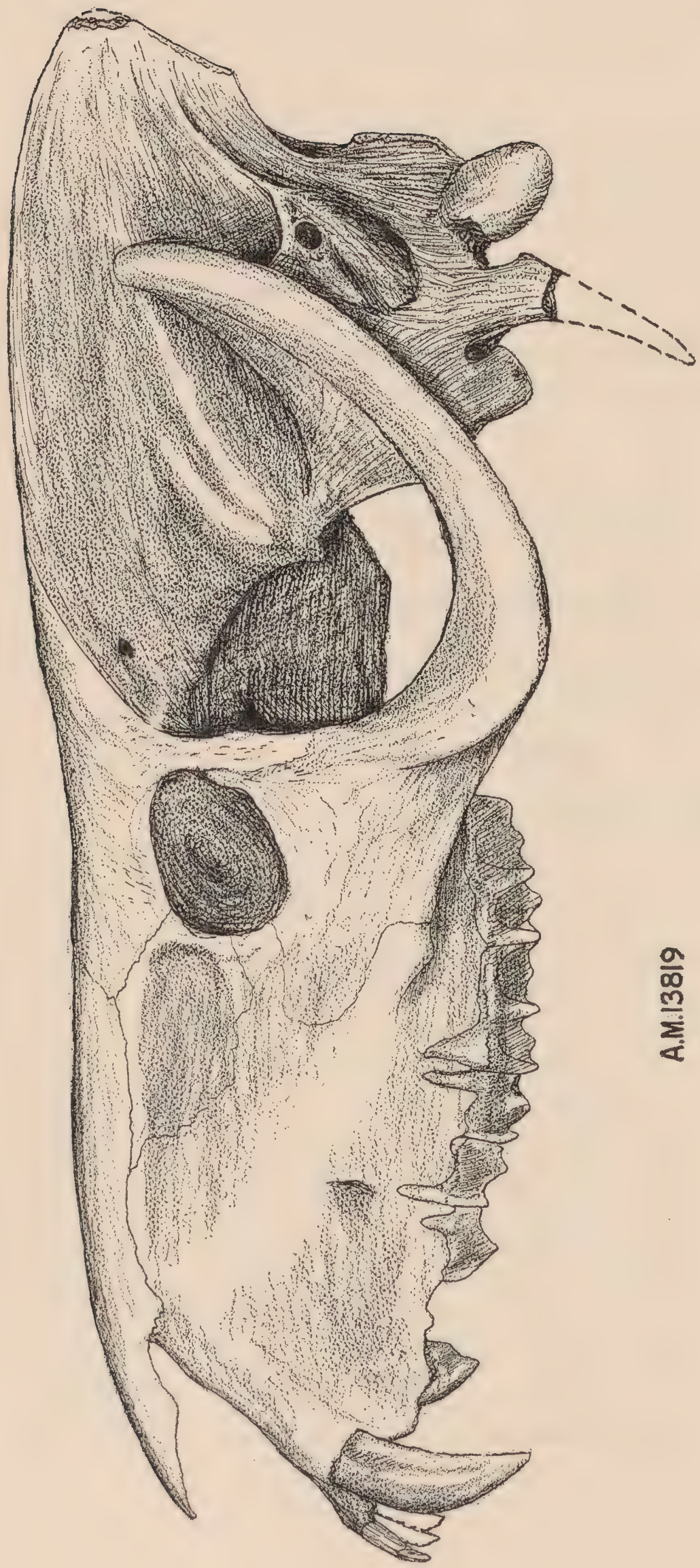
To this genus has already been assigned a bewildering number of species, from the John Day, Monroe Creek, Lower Harrison, Deep River and certain Montana beds. The American Museum material from the Lower Rosebud formation consists of over twenty skulls, together with considerable skeletal material. On examining this material it at once became clear that either there were five or six species in this one formation or that there was marked sexual dimorphism, as well as considerable individual variation. A careful examination of the two largest types resulted in drawing them superimposed to make figure 9. To me, this indicates that, while No. 13819 and No. 12948 differ in the amount that the incisors protrude, the size of the canines, the width of the zygomatic arch and the length of the posterior projection of the supra-occipital crest, still they are alike in the premolar and molar dentitions, the width of the snout, the position of the orbits and ear openings, the bullæ and the base of the skull. The latter list of characters is of deep-seated features, such as do not change with minor changes of habit, while the first list is entirely of characters which do change where there is sexual dimorphism. I have concluded that in this genus there is wide sexual dimorphism, and

Genera of Oreodonts, their Respective Geological

	AGE	SKULL	BULLÆ	POSTPTERYGOID PROCESS
<i>Protoreodon</i>	Upper Eocene (Uinta)	mesocephalic; open orbit	tiny	moderately oval
<i>Oreonetes</i>	Lower Chadron	mesocephalic; open orbit	tiny	small and oval
<i>Merycoidodon</i>	Upper Chadron to Middle Oligocene	mesocephalic; closed orbit	tiny	moderately oval
<i>Limnenetes</i>	Lower Chadron	mesocephalic; open orbit	large	small and oval
<i>Eporeodon</i>	Middle Oligocene to Lower Miocene	mesocephalic; closed orbit	medium large	moderate and oval
<i>Mesoreodon</i>	Lower Miocene	dolichocephalic; closed orbit	medium large	small, oval and long
<i>Promerycochærus</i>	Lower to Middle Miocene	dolichocephalic; closed orbit	large	stout, oval and short
<i>Merycochærus</i>	Upper Harrison to Middle Miocene	brachycephalic; closed orbit	medium large	very wide and flattened
<i>Pronomotherium</i>	Upper Miocene to Pliocene	brachycephalic; closed orbit	small, cylin- drical	wide and flattened
<i>Merycoides</i>	Lower Miocene	dolichocephalic; closed orbit	medium large	moderate and oval
<i>Phenacocælus</i>	Lower Miocene	mesocephalic; closed orbit	large	large and oval
<i>Ticholeptus</i>	Lower Miocene to Pliocene	mesocephalic; closed orbit	large	wide and flattened
<i>Merychys</i>	Lower Miocene to Pliocene	brachycephalic; closed orbit	large	small and flat- tened
<i>Leptauchenia</i>	Upper Oligocene to Middle Miocene	brachycephalic; closed orbit	enormous	tiny and flattened
<i>Cyclopidius</i>	Lower Miocene to Middle Miocene	brachycephalic; closed orbit	enormous	tiny and flattened

Horizons and their Diagnostic Skull Characters

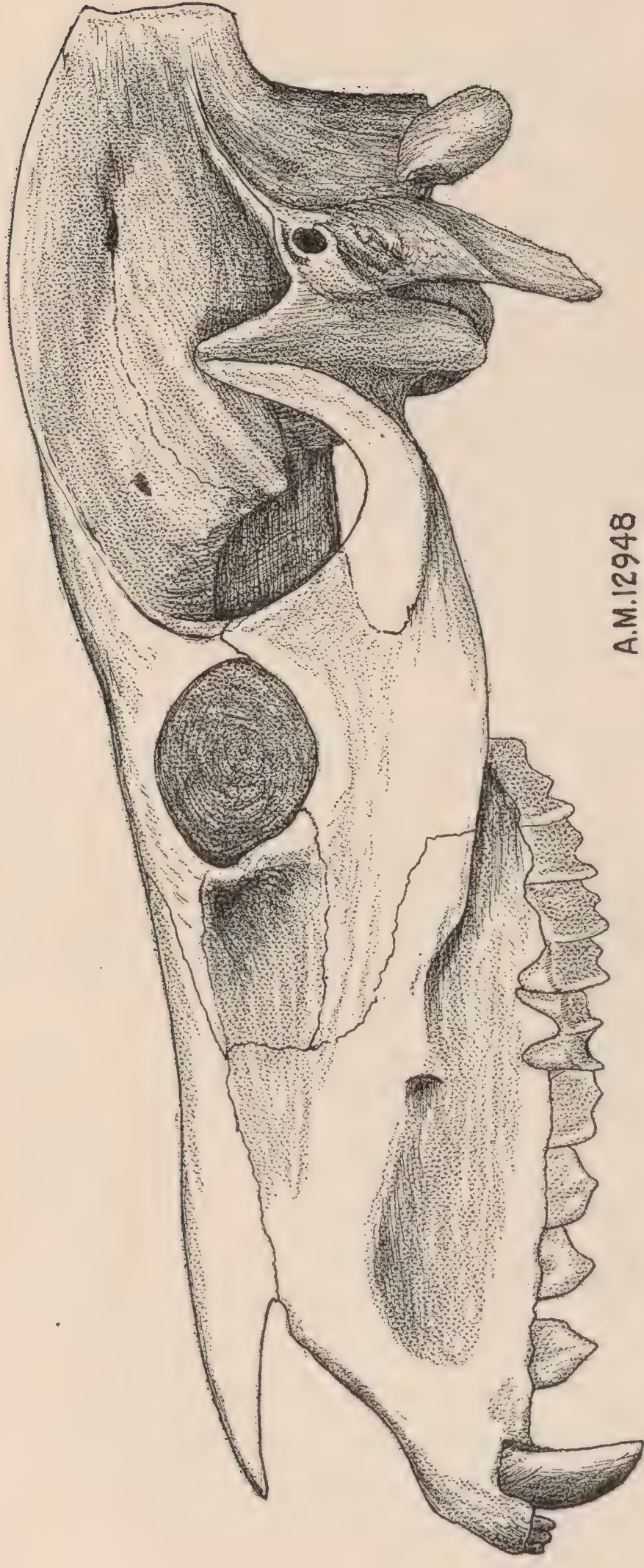
ZYGOMATIC ARCH	EXOCCIPITAL BONES	NASAL BONES	ANTORBITAL PIT OR VACUITY
light	supraocc. crest prolonged behind	long	neither
light	supraocc. crest moderate	long	neither
light	supraocc. crest prolonged behind	long	shallow pit
light	occiput wide; crest not prolonged	long	pit
light	supraocc. crest high and prolonged	long	pit
light	supraocc. crest high and prolonged	long	pit
heavy and wide	supraocc. crest high and prolonged	long	pit
heavy and wide	supraocc. crest none	greatly shortened	pit
medium and wide	supraocc. crest moderate	greatly shortened	pit
light	supraocc. crest low, not prolonged pits	long	pit
light	supraocc. crest low, little prolonged pits	long	pit and big vacuity
light	supraocc. crest moderate, little pro- longed	long	vacuity
light and fairly wide	supraocc. crest low, not prolonged pits behind	long	pit and small vacuity
light and very wide	occiput very broad	fused to maxilla	enormous vacuity
heavy and very wide	occiput very broad	fused to maxilla	enormous vacuity



A.M.13819



Fig. 10. *Promerycochaerus thomsoni*, male, skull and upper dentition of the type. Two-fifths natural size.



A.M.12948



Fig. 11. *Promerycochærus thomsoni*, female, skull and lower dentition of No. 12948. Two-fifths natural size.

that the width of the arches changes not only with sex, but also with age. I have therefore reduced the number of Lower Rosebud species to three, describing both males and females.

I am convinced that the same applies to the large number of species described from the John Day beds, and I would use the length of the molar and premolar series as a basis of comparison, considering such features as the width of the arches, the size of the canines, or their protrusion as sex or individual variations.

***Promerycochoerus thomsoni*, new species**

This is the largest of the Rosebud species, and I have selected No. 13819 of the American Museum as the type, associating No. 12948 with it as the female. The male skull is from Eagle Nest Butte, and the female from Wounded Knee Creek, both of South Dakota and the same bed. The name is in honor of Mr. Albert Thomson, veteran collector in this region and finder of the male skull. Other skulls of the male type are Nos. 13818, 12944 and 12951.

The species is characterized by a broad snout, with large but shallow antorbital fossæ. The brain case is somewhat inflated, with a marked ridge across the inflated parietal region. Upper premolars 3 and 4 and molar 1 all have cingula on the outer side of the teeth. The lower premolars are typically those of the genus (see Fig. 5), except that premolar 3 has the posterior intermediate crest rising from about the middle of the median crest, instead of from the primary cusp.

In the various Lower Miocene beds there are several large *Promerycochæri* about the size of this species. *P. grandis* from the Canyon Ferry beds is of the female type, but is not only larger than *P. thomsoni* but also has a much narrower skull and arches, and has the snout markedly prolonged, especially the premolar region. *P. macrostegus* of the Upper John Day is a male type and about the same length as our species, but it has a very small antorbital fossa, where *P. thomsoni* has a broad one and smaller bullæ, and the whole skull is narrower. *P. latidens* of the John Day has about the same over-all measurement as the male of *P. thomsoni*, but its snout is short and the dentition compressed. *P. marshi* of the John Day is of the female type, but is both larger and longer than the female from the Lower Rosebud. The following table gives the most important measurements for comparison with nearly related species. Other measurements may be taken directly from the drawings.

	<i>P.</i> <i>thom-</i> <i>soni</i> ♂	<i>P.</i> <i>thom-</i> <i>soni</i> ♀	<i>P.</i> <i>grandis</i> ♀	<i>P.</i> <i>macro-</i> <i>stegus</i> ♂	<i>P.</i> <i>latidens</i> ♂	<i>P.</i> <i>marshi</i> ♀
Length of the skull	388	362	390	380	385	380
Width of the skull	277	224	186	246	279	344
Length of the upper molar series	82	78	98	81	79	85
Length of the upper premolar series	66	73	82	71	695	76

***Promerycochærus gregoryi*, new species**

This is the medium-sized form in the Lower Rosebud and the one found in largest numbers. For the type I have chosen No. 12964, a skull and lower jaw, the skull being slightly crushed laterally as shown in the figure. This is a female, a narrow skull with light arches, which are estimated to have had a width of 190 mm. No. 12962 belongs to the same species and is also a female. No. 12816 is slightly longer and with wider, heavier arches, and is the male of this species. The type comes from Porcupine Creek, South Dakota. The name is in honor of Dr. W. K. Gregory, who was a member of the expedition which collected this material.

This species is characterized by its size, rather deep and broad ant-orbital fossæ, an elongated brain case, moderate-sized bullæ, and the fact that for this genus the premolars, both upper and lower, are quite simple. On lower premolar 3 the posterior intermediate crest runs from the primary cusp, as is normal for the genus.

This species approaches *P. hollandi* of the Canyon Ferry beds in size, but it has a deeper antorbital fossa, and a shorter snout and dentition. *P. chelydra* of the Upper John Day is a male of similar size but has a much longer snout and dentition. *P. leidyi* is another John Day species which approaches our Rosebud form in length of skull, but it too has a longer snout and dentition. I presume *P. chelydra* and *P. leidyi* represent the male and female of a *Promerycochærus* in the John Day, which is perhaps the nearest of any species to *P. gregoryi*.

The following table gives principal measurements and comparisons with the nearest related species.

	<i>P. greg-</i> <i>oryi</i> ♂	<i>P. greg-</i> <i>oryi</i> ♀	<i>P. hol-</i> <i>landi</i> ♂	<i>P. chely-</i> <i>dra</i> ♂	<i>P. leidy-</i> <i>yi</i> ♀
Length of the skull	344	313	342	342	330
Width of the skull	235	190	234	256	188
Length of the upper molar series	79	70	76	78	76
Length of the upper premolar series	60	58	70	63	48



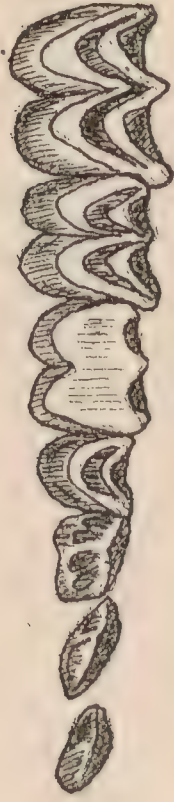
A.M.12964



Fig. 12. *Promerycochærus gregoryi*, female, skull, upper and lower dentitions, from the type. One-half natural size.



A.M.12967



A.M.12968

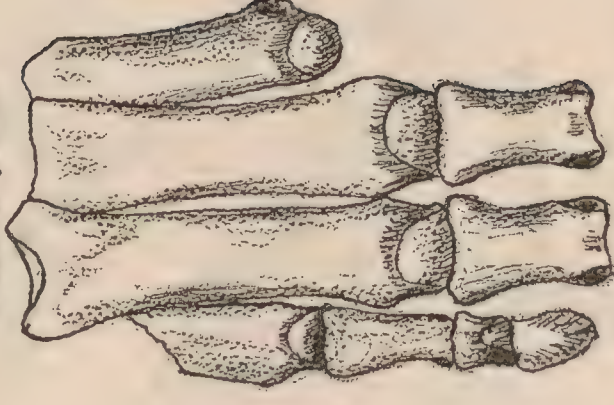
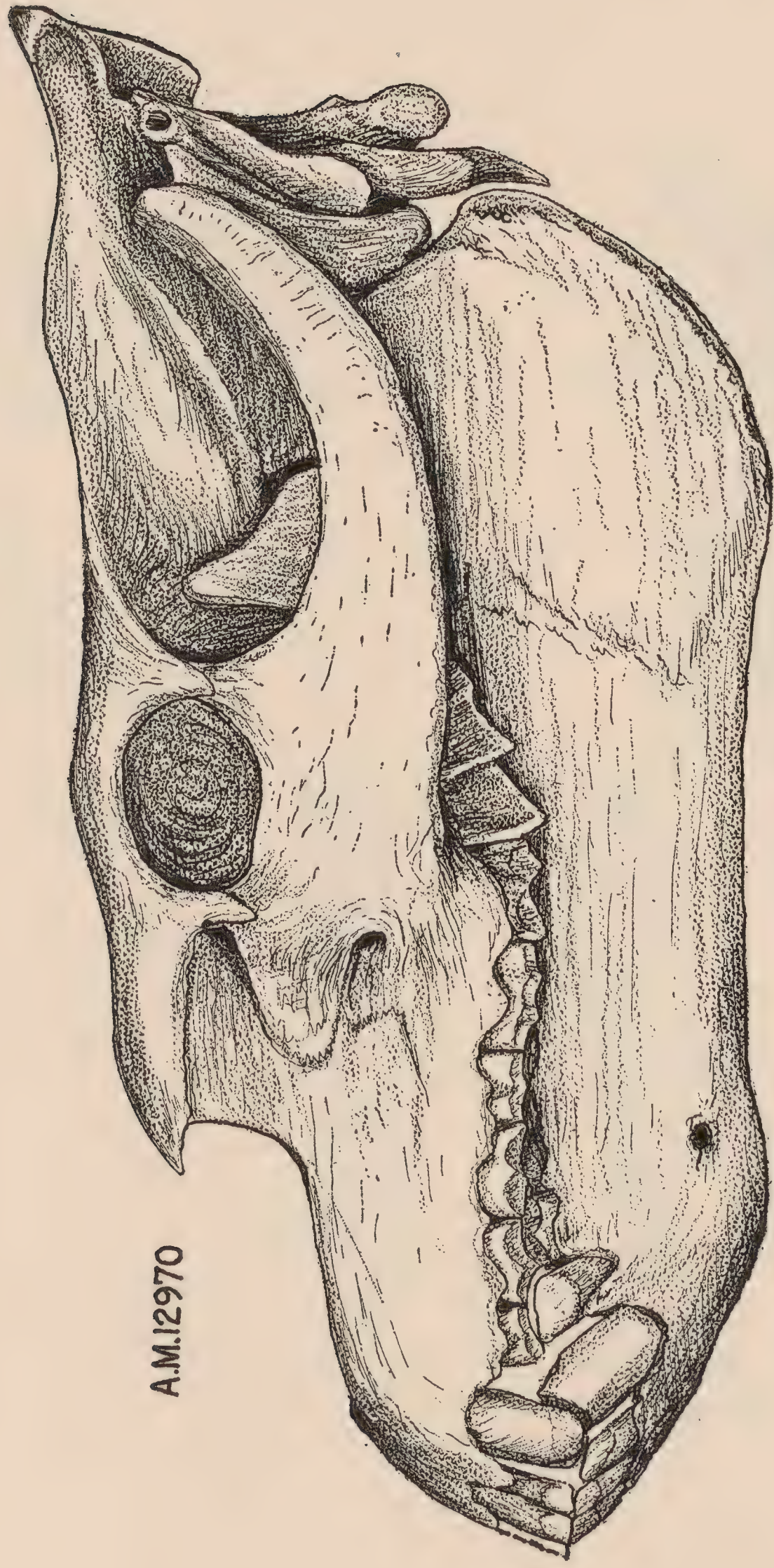


Fig. 13. *Promerycochærus pygmyus*, female, skull and upper dentition from the type. One-half natural size. Front foot from No. 12968. One-half natural size.



A.M.12970

Fig. 14. *Merycochærus matthewi*, skull from the type. One-half natural size.

Promerychoærus pygmyus, new species

This is a tiny species, the smallest of the true *Promerychoæri*, but it has the characters of the genus not only well developed but in an advanced degree. It is a dwarf species rather than a primitive one. I have chosen No. 12967 as the type of the species, a female found on Porcupine Creek, South Dakota. No. 12968 is a second female of this species, having an imperfect skull, but with good fore feet and some other limb bones. No male has yet been found of this species.

The specific characters are the small size; small bullæ; a wide snout with broad and shallow antorbital fossæ; simple, rather narrow teeth; and an extremely short foot.

There are no other species at all close to this one.

The following measurements of the principal parts will serve to identify the species.

Length of the skull	253 mm. rear estimated, see figure 12.
Width of the skull	179
Length of the upper molar series	59
Length of the upper premolar series	48

MERYCOCHÆRUS

In his description of *Merychoærus proprius*, the type species of this genus, Matthew¹ showed that this was a highly specialized genus in that the cranium was shortened and broadened; the nasals moved far toward the rear; the zygomatic arches heavy and wide, and the limbs short and stocky. So far only one species has been described, but the material in the American Museum furnishes us with two new species. The genus appears abruptly with the Upper Harrison and disappears as abruptly in the Martin Canyon beds.

Merychoærus matthewi, new species

This species is from the Upper Rosebud beds and was found three miles northeast of Porcupine Butte, South Dakota. I have used No. 12970 as the type, a skull and jaws with a good front limb and some other less perfect limb bones. The name is in honor of Dr. W. D. Matthew, who found the Upper Rosebud beds.

The specific characters are: the size; the fact that the sagittal crest extends to the rear of the skull and unites with the lambdoidal crests in making the projection behind, whereas in other species the sagittal crest

¹1898. Mem. Amer. Mus. Nat. Hist., I, p. 401.

does not extend to the lambdoidal crests (compare with *M. magnus* and *M. proprius*); the broad upper teeth; and the relatively long limbs and feet.

I here introduce a comparison of the three known species.

	Length of skull	Width of skull	Length of upper molars	Length of upper premolars	Length of humerus	Horizon
<i>M. matthewi</i>	299	220	87	65		U. Rosebud
<i>M. proprius</i>	286	244	88	61		Pawnee Cr.
<i>M. magnus</i>	334	273	95	68	240	U. Harrison

	Length of radius	Length of metacarpal IV	Length of femur	Length of tibia	Length of metatarsal IV	Horizon
<i>M. matthewi</i>	146	71				U. Rosebud
<i>M. proprius</i>	150	63	250	195	68	Pawnee Cr.
<i>M. magnus</i>	161	66	238	195	65	U. Harrison

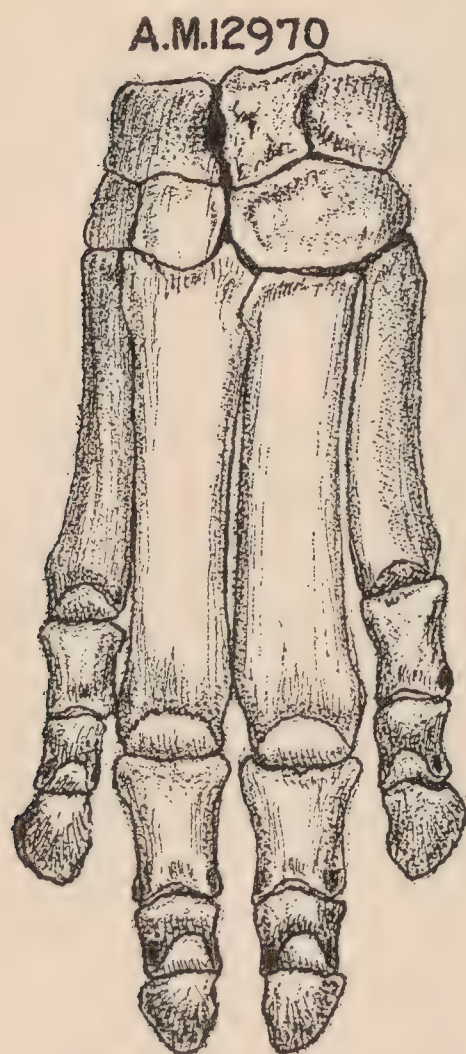


Fig. 15. *Merycochoerus matthewi*, carpus and fore foot from the type. One-half natural size.

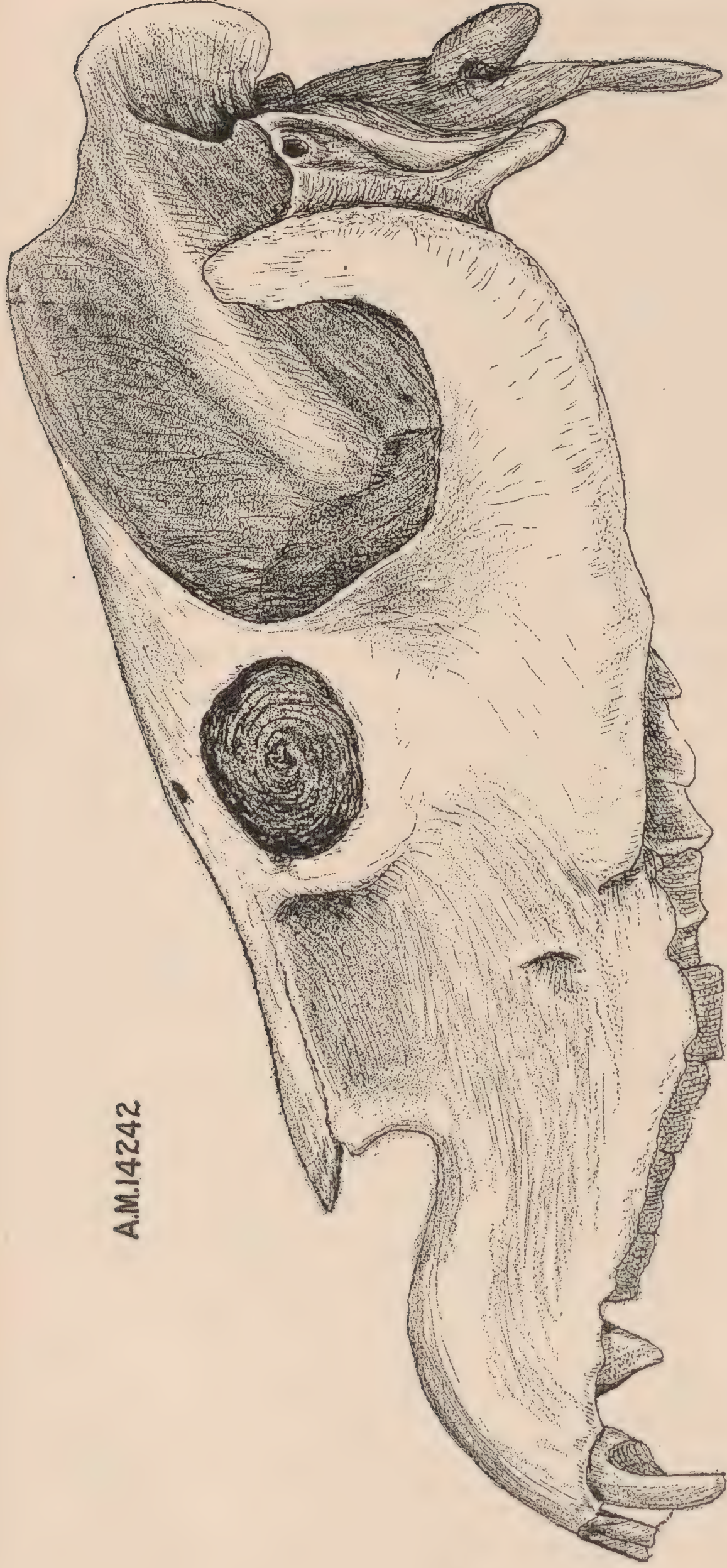
From the above it is seen that *M. matthewi*, while small, does not have as short or stocky limbs and feet as do the other two species. The skull also is much less shortened and less broadened than is the case in the other two species. Furthermore, in this species there is not, as yet, a tendency, which is so marked in the other two species, toward dishing in the nasal region. The line of the top of the skull is more or less parallel to that along the top of the premaxillæ, whereas in the other two species the nasals slope down as though to meet the premaxillæ.

***Merycochoerus magnus*, new species**

The type for this species is No. 14242, from the Upper Harrison beds, seven miles northeast of Agate, Nebraska. The type is an old individual, but with it are associated both front and hind limbs. It is by no means a rare species in these beds.

This species is nearer to *M. proprius*, in that the sagittal crest ends some distance in front of the lambdoidal region. The brain case is greatly shortened and broadened, and the whole rear of the skull is crowded together. The zygomatic arches are heavy and wide, but not as wide proportionally as those of *M. proprius*. There is a moderate antorbital fossa.

A.M.14242



A.M.14238



Fig. 16. *Merycochærus magnus*, skull from the type, upper and lower dentitions from No. 14238. One-half natural size.

The line along the top of the skull pitches down toward the front, so that the nasals approach the much dished premaxillæ. The limb bones have the same character as in *M. proprius*, being heavy and stocky, with the feet extremely short and stubby. The phalanges go to the extreme in their shortening.



Fig. 17. *Merychoærus magnus*, front foot from the type. One-half natural size.

MERYCHYUS

This genus, in which there has been constant confusion, is based on the species *M. elegans* and consists of a series of small light-built oreodonts, ranging from the Lower Rosebud and John Day up into the Pliocene, from which horizon the type species came. I should redefine the genus as follows.

Merychys is a genus of Oreodontidæ of light build; with slender limbs; having a wide brachyodont skull with light zygomatic arches; large bullæ; and low sagittal and lambdoidal crests, which are not prolonged behind. The back of the skull is broad, with either deep pits or vacuities in the exoccipital bones. There is usually a large antorbital fossa, often with a small vacuity between the lachrymal, frontal and maxillary bones. The upper premolars are greatly shortened, which is due to the anterior portion of these teeth being reduced, in the later species often to a point where the median crest may be taken for the anterior crest, which makes the tooth seem to stand transversely in the jaw. Peterson¹ has recently figured a complete skeleton of this genus, *Merychys minimus*.

The type species of this genus, *M. elegans* Leidy, was found on the Niobrara River in Nebraska, in Hayden's horizon F, which was described as Pliocene. This seems to be the Valentine beds of Lower Pliocene age. A large number of species were referred to this genus, almost always based on teeth alone, and most of them either have already been or must in the future be, referred to other genera, most often to *Ticholeptus*. Below I have listed all the species which really belong to the genus. I include Thorpe's *Oreodontoides oregonensis* from the John Day as a primitive representative. His *Paroreodon marshi* seems to be distinct, though related. Besides there being too many forms referred to this

¹1923. Annals Carnegie Museum, XV, p. 96, Pl. VIII.

genus, there has been some identification of species as *M. elegans* in more than one horizon, which a study of the premolars serves to straighten out. The following table will serve to show how extremely conservative this genus has been.

		Length of skull	Length of upper molars	Length of upper premolars
<i>M. (Oreodontoides) oregonensis</i>	Upper John Day	165	33	30
<i>M. curtus</i>	Lower Rosebud	158	37	30
<i>M. siouxensis</i>	Lower Harrison	178	46	35
<i>M. minimus</i>	Upper Harrison	160	39	30
<i>M. leptorhynchus</i>	Laramie Peak	167	43	38
<i>M. arenarum</i>	Laramie Peak	191	45	38
<i>M. delicatus</i>	Upper Rosebud	140	36	31
<i>M. parigonus</i>	Deep River		50	
<i>M. paniensis</i>	Pawnee Creek			
<i>M. elegans</i>	Valentine		45	31

		Length of lower molars	Length of lower premolars
<i>M. (Oreodontoides) oregonensis</i>	Upper Day John		
<i>M. curtus</i>	Lower Rosebud	40	33
<i>M. siouxensis</i>	Lower Harrison		
<i>M. minimus</i>	Upper Harrison	43	30
<i>M. leptorhynchus</i>	Laramie Peak	46	32
<i>M. arenarum</i>	Laramie Peak	46	32
<i>M. delicatus</i>	Upper Rosebud	39	29
<i>M. parigonus</i>	Deep River	51	
<i>M. paniensis</i>	Pawnee Creek	47	35
<i>M. elegans</i>	Valentine	47	34

In order to make a basis for the comparison of the different species of this genus, I here figure the premolars of the upper jaw of the paratype of *M. elegans*, the type being too worn to show the character of these teeth. This is from the jaw figured by Leidy, 1869, Jour. Acad. Nat. Sci. Phila., VII, Pl. XI, fig. 3.

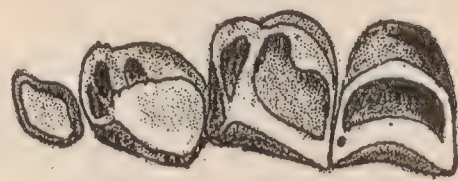


Fig. 18. *Merychys elegans*, from Leidy's paratype (see text). Natural size.

***Merychys curtus*, new species**

The type of this species is No. 13817 in the American Museum and was found ten miles east of Kyle, South Dakota, in the Lower Rosebud beds.

While a typical *Merychys*, it is smaller than most of the species. It has enormous bullæ and a deep antorbital fossa with a small vacuity



A.M.13817



Fig. 19. *Merychyrus curtus*, skull and lower jaw from the type. One-half natural size.



A.M.13817



Fig. 20. *Merychyrus curtus*, upper and lower dentitions, from the type. Natural size.

just above it. The whole skull seems foreshortened. The teeth are wide and short from front to back. The upper premolars are characterized by the anterior portion's being abbreviated and having several small striæ running forward from the primary cusp, giving this anterior end a striated appearance. The posterior crescent is well developed but does not unite with the median crest. Premolar 4 has a small pit in the anterior external corner. The lower premolars are those typical of the genus.

As compared with other species, this is about the size of *M. minimus*, but this species has a large antorbital fossa and a small vacuity, whereas *M. minimus* has a small fossa and a large vacuity. *M. curtus* is a little larger than *M. delicatus*, which is, however, lighter-built throughout and has only a slight antorbital fossa and no vacuity.

***Merychys siouxensis*, new species**

The type for this species is a fine skull in the American Museum, No. 13774, from the Lower Harrison beds, ten miles west of Agate, Nebraska. It is not far from *M. elegans* in size, which name has been incorrectly applied to some of the material in the Lower Harrison beds, *M. elegans* coming from the Valentine beds.

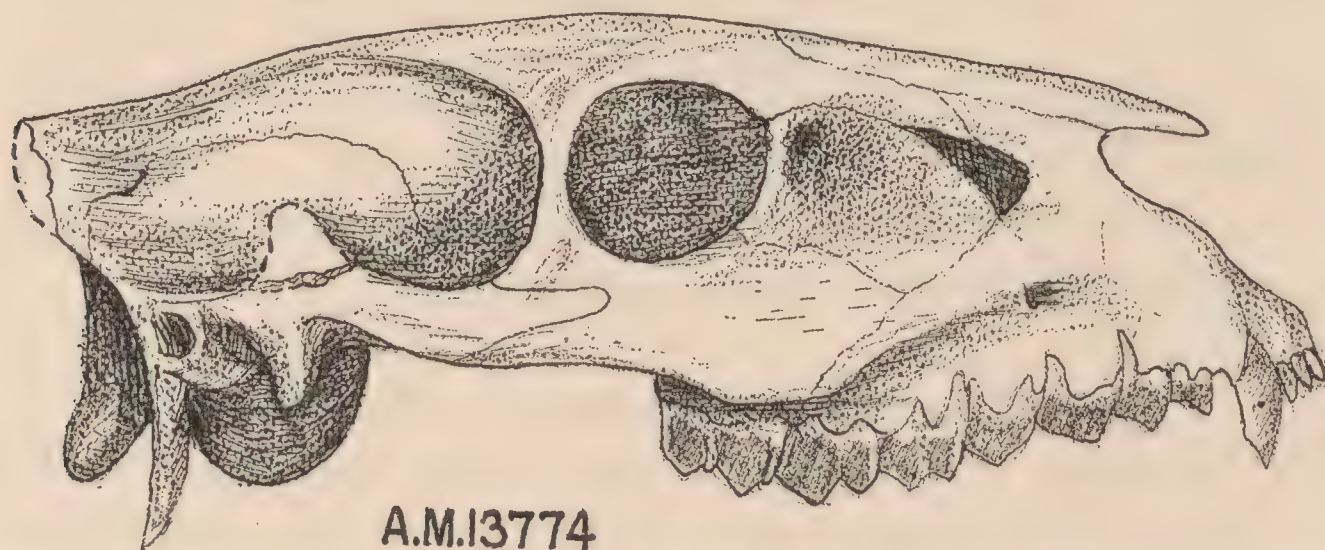


Fig. 21. *Merychys siouxensis*, skull from the type. One-half natural size.

The specific characters are a moderately large antorbital fossa and a moderate-sized antorbital vacuity. The premolars are neither crowded in the jaw nor shortened, as are those of *M. elegans*. This is also about the same size as *M. paniensis*, which species is lighter-built throughout and has a much narrower dental series. These three species are nearly the same size, but a careful examination of the upper dental series of premolars will readily distinguish them. In *M. siouxensis* the anterior portion of premolars 2 and 3 is (for this genus) long, and the anterior basin is divided into two parts.

***Merychys delicatus*, new species**

This species is based on a skull and jaws, numbered 12980 in the American Museum, found on Porcupine Creek, South Dakota. It is the smallest species known and at the same time has the best-marked specific characters.

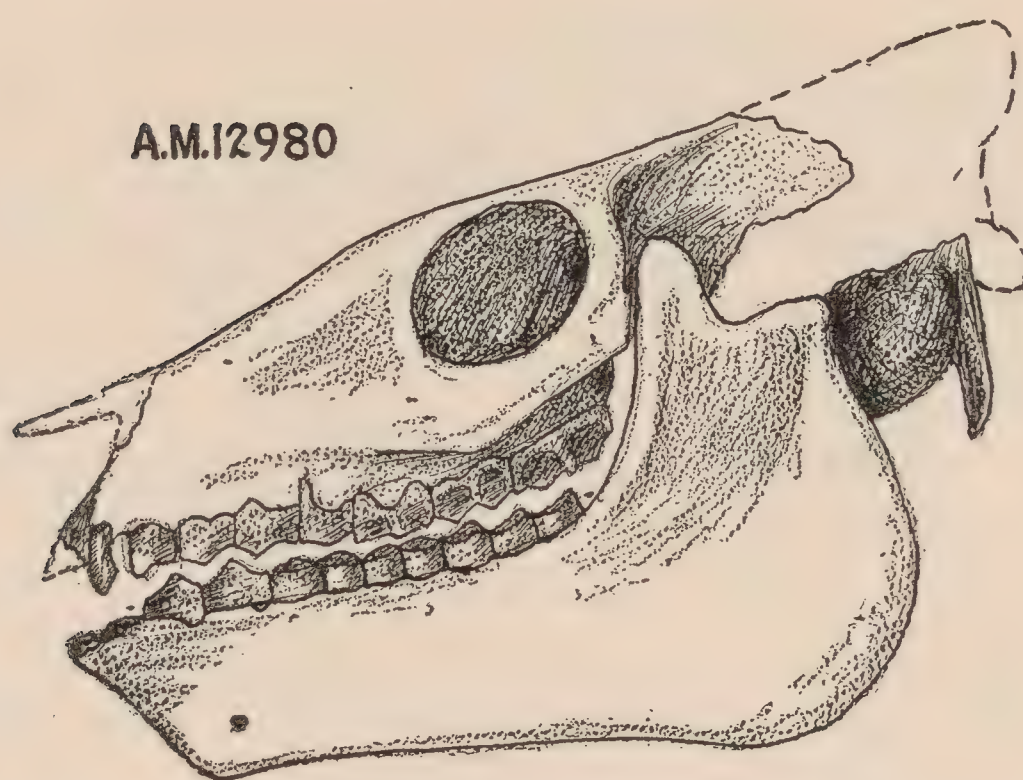


Fig. 22. *Merychyrus delicatus*, skull and jaws from the type. One-half natural size.

The specific characters are: the size; the light build; only a trace of an antorbital fossa, and no vacuity. There is no crowding or special shortening of the premolars. With the measurements in the table on page 31, the species will be readily recognized.

***Merychyrus paniensis*, new species**

Merychyrus elegans MATTHEW, 1898, Mem. Amer. Mus. Nat. Hist., I, p. 419.

The material on which this species is based is that which was used by Dr. Matthew in describing the Pawnee Creek fauna. I have chosen No. 9047 of the American Museum as the type for the species, because that is



Fig. 23. *Merychyrus paniensis*, lower jaw from the type. One-half natural size.

an adult lower jaw associated with metapodials of both the fore and hind feet and other bones. No. 9442 is an imperfect skull, but it is young; No. 9045 is another lower jaw, with some limb material; No. 9046 has the nearly perfect front foot, illustrated in Fig. 24, and No. 9443 has an equally good hind foot. All show the slender and delicate build of this species.

The species is very similar to *M. elegans*, but the upper dentition, so far as known, is so largely deciduous that comparisons can not be made on this character. The lower dentitions, however, can be compared. While the length over all of the two premolar series is nearly the same, in *M. paniensis* the first lower premolar is considerably smaller; premolar 2 is considerably larger; premolar 3 somewhat larger, and premolar 4 of about the same size. The whole dentition of *M. paniensis* is lighter, both the premolars and the molars being narrower.



A.M.9046

Fig. 24.

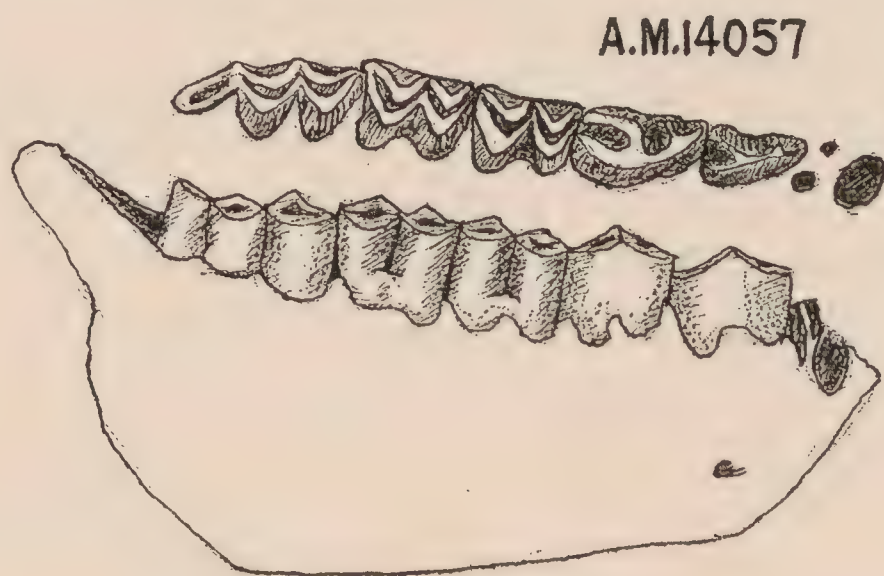


Fig. 25.

Fig. 24. *Merychyrus paniensis*, front foot from No. 9046. One-half natural size.

Fig. 25. *Ticholeptus hypsodus*, lower jaw from the type. One-half natural size.

TICHOLEPTUS

This genus was established to include those oreodonts with limbs of intermediate length and with skulls of a mesocephalic or brachycephalic type, on which the supra-orbital crest is high, the exoccipital region broad, the bullæ large, and the antorbital vacuity large. The teeth are shortened from front to back, and the lower fourth premolar is distinguished by having the anterior crest bifurcated at the front end. It ranges from the Lower Harrison beds up into the Snake Creek.

Ticholeptus hypsodus, new species

This is one of the oreodonts from the Snake Creek beds, twenty-three miles south of Agate, Nebraska. I have taken No. 14057, a lower jaw, as the type. The pattern of the teeth is that typical of *Ticholeptus*,

but these are more hypsodont than is usual for the genus. This, however, seems to me simply the expression of the advanced condition of these late forms, and it is not desirable to separate them from their predecessors in the Miocene.

The lower premolars have the anterior crest bifurcated, as is characteristic of the genus, but in this species the fourth premolar is slightly peculiar in that the posterior basin is not completely inclosed until the tooth is much worn. Molars 2 and 3 are characterized by having a cingulum in the gap between the two lobes on the outside of each tooth.

METOREODON

This genus was established by Matthew and Cook¹ for several oreodonts in the Snake Creek beds which at the time they associated with *Merychys*. The type species of the genus is *M. relictus*, which represents an exaggeration of the *Ticholeptus* characters. The teeth are more hypsodont. The cusp-like pillar on lower premolar 4 has grown forward and enlarged so that it almost fills the anterior basin. The furrows on the outer side of the premolars are also distinctive.

Metoreodon profectus is a larger specialized form which I should refer to *Ticholeptus*.

EPOREODON

This genus, so abundant in the Upper Oligocene and John Day beds, has, so far as known, but one representative in the Miocene of the eastern Rocky Mountain district.

Eporeodon relictus, new species

The type of this species, No. 13813 in the American Museum, was found in the Lower Rosebud, six miles west of American Horse Creek, South Dakota. Other specimens of the same species are No. 13814 and No. 8949, with the latter of which there is a considerable part of the skeleton, but unfortunately the individual is a young one.

The skull is characterized by being nearly straight along the top, with bullæ of medium size, a small and rather deep antorbital fossa, and teeth typical of the genus. There is an unusually wide gap between the postglenoid and paroccipital processes, so that the whole tympanic bone is exposed in the side view.

¹1909. Bull. Amer. Mus. Nat. Hist., XXVI, p. 391.

E. montanus is the only eastern form of similar size, but it is larger and has an arched line along the top of the skull. *E. occidentalis* of the John Day is similar in size, but this species has a skull of much wider and heavier build.

The front limb is light and slender, even for a member of this genus, but would fall in the class described as medium, that is, about the weight of the skeleton of *Merycoidodon*. The following measurements give the characteristics of the species.

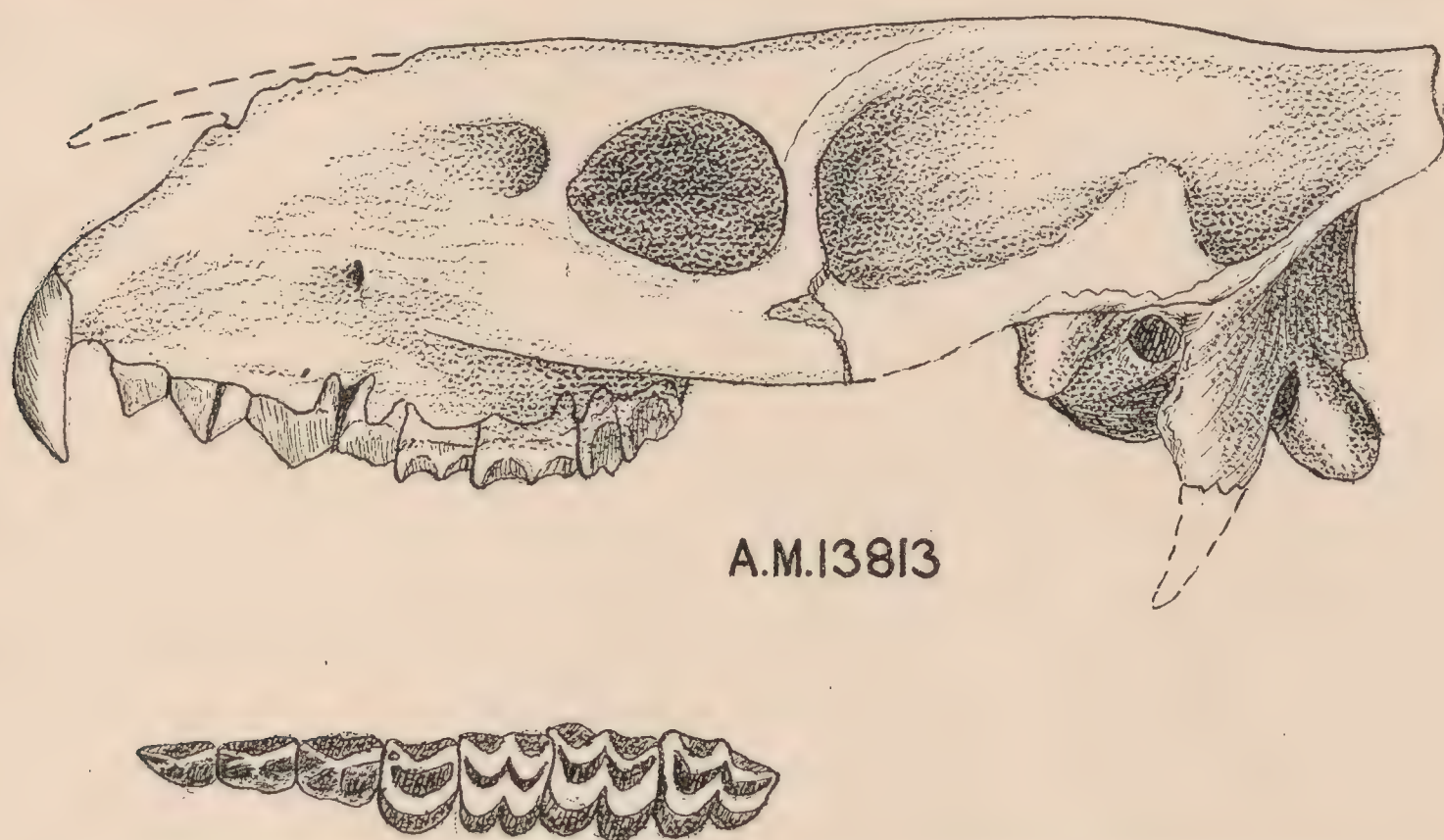


Fig. 26. *Eporeodon relictus*, skull and upper dentition from the type. One-half natural size.

Length of the skull	198 mm.
Length of upper molar series	44
Length of upper premolar series	40
Length of radius (No. 8949)	100
Length of ulna (No. 8949)	135
Length of metacarpal III (No. 8949)	52
Length of first phalanx (mc. III) (No. 8949)	17
Length of second phalanx (mc. III) (No. 8949)	11
Length of ungual phalanx (mc. III) (No. 8949)	13

Article II.—ON THE CLASSIFICATION OF THE REPTILES¹

BY R. BROOM

DEDICATED TO THE MEMORY OF SAMUEL WENDELL WILLISTON

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INTRODUCTION

One of Professor Williston's latest papers, published the year before his death, gives what may be regarded as his final conclusions on the very difficult subject of the "Phylogeny and Classification of Reptiles." No one recognized more fully than Williston the difficulties of making a satisfactory classification when so many of our types are little more than fragments, and he rather discouraged the attempts made by others. He

¹This and the following paper were written in 1919 with the view to their forming part of a proposed memorial volume, which was to be issued in honor of the late Samuel Wendell Williston. For various reasons, the project had to be abandoned, but I trust these papers will, at least, serve as a small wreath offered by one scientist to the memory of another.

From 1903 for ten years, Williston and I corresponded very regularly and threshed out many of the problems of the Permian reptiles and their affinities. I kept him constantly informed of all advances in South African paleontology, and he let me know of all that was being done in America. I met him when he was in London in 1913 and spent a most enjoyable time with him.

During the war our correspondence was interrupted but on my return to South Africa was resumed. Shortly before his death, he wrote me about his illness and, from the symptoms he described, I recognized the case as probably very serious,—more serious than he apparently believed. I wrote with much anxiety as to his condition, but he probably passed away before my letter arrived.

In all branches of science, America has played a very important part, but in paleontology in the past fifty years she has stood preëminent. Leidy, Marsh and Cope made paleontology almost exclusively an American science. Williston has done much to continue this preëminence, and when the history of the science comes to be written, Williston's name will be placed beside those of these other immortals.

says, "It is only hesitatingly that I have ventured, for the first time, to express in tabular form my own views."

Personally I have always considered that something was gained by even a very provisional classification which might contain much error. Professor Osborn's classification of 1903 has a good many things in it to which exception might be taken, and yet the main truth that it emphasized, that most reptiles can be divided into two subclasses, remains well established, and his groups Synapsida and Diapsida are with some slight modifications accepted by most workers including Williston himself, though for a time he objected to them.

Each classification has helped us a little farther on the road and the very free criticism of each has perhaps helped nearly as much; and I am very sure that, were Williston still with us, a very full and frank criticism of his latest classification would be much more pleasing to him than a mere blind acceptance of it as it stands.

In the classification of the reptiles there are only a few important points that remain in doubt, apart from the attempt to place forms that are very imperfectly known, such as *Eunotosaurus* or *Broomia* or *Mesosaurus*, and of these we need consider at length only the lizards, the chelonians and the plesiosaurs.

THE TEMPORAL BONES OF THE LIZARDS

By most scientists the lizards have been regarded as descended from some two-arched reptile somewhat resembling *Sphenodon*, but which lost the lower temporal arch and came to have a loose quadrate. Williston believed that the Squamata have no near relationships with the Diapsida, having sprung quite independently from a different cotylosaurian ancestor, and that they only resemble the rhynchocephaloid forms by convergence. He believed that *Aræoscelis*, with a single upper temporal fossa, had a type of skull from which the lacertilian was derived by "simple emargination of the broad lower temporal arch." Watson, though he does not wholly agree with Williston, also believes that the temporal arch of the lizard does not correspond to the upper arch of the Diapsida, but is really a latero-inferior arch thinned out from below and thus really homologous with the two arches of *Sphenodon*.

The two points in the structure of the lacertilian skull which have given rise to differences of opinion are, the nature of this temporal arch and whether it is homologous with the upper arch of *Sphenodon*, and the nature of two bones which lie above the quadrate in the post-temporal region. And on the solution we find to the latter problem, depend, to a considerable extent, the conclusions we must come to on the former.

In a typical lacertilian, such as *Varanus*, there are two bones, each of which has its posterior and lower end wedged in between the top of the quadrate and the outer end of the paroccipital. The outer bone passes upward and then forward and forms a long articulation with the post-orbital. The inner passes upward and forward and clasps the lower part of the posterior process of the parietal.

In agamids the outer bone articulates in front with both the post-orbital and the jugal and has an inner process which overlaps both the inner bone and the parietal. The inner bone lies mainly underneath the parietal, but it has a fairly large articulation with the paroccipital and also with the quadrate.

In many lizards one of the two bones is missing, but, as two are present in very different suborders or families, it is manifest that two bones in this region is the primitive condition.

It will be unnecessary to consider all the different interpretations that have been given to these two bones. The inner one has been regarded as the squamosal by Gegenbaur, Baur, Gaupp and Watson; the outer has been held to be the squamosal by Huxley, Parker, Cope, Boulenger and Williston. By Owen, Gegenbaur, Baur and Watson the outer bone has been considered to be the quadratojugal. Huxley, Parker, Cope and Boulenger have looked on the inner bone as a supratemporal, while Williston has identified it with the tabular. For many years, I held the opinion of Gaupp that the inner bone was the squamosal and the outer a new element which might be called prosquamosal or paraquadrate, but in 1913, as a result of the study of pythonomorph skulls in the American Museum, I became convinced that the outer bone must be looked upon as the squamosal, and the inner, as held by Williston, the tabular.

As the study of the lizard skull has led to such varied opinions, it is necessary to look to other forms for further help.

Watson thinks that the skull of *Pleurosaurus* in the British Museum specimen supports his conclusion that the outer bone is the quadratojugal and the inner the squamosal. A few years ago, I also examined this specimen but did not think Watson's conclusions were justified. The specimen as preserved is crushed very flat, and, while showing well the top of the skull, it gives no clear idea of the sides. Watson gives a side view restoration and makes the skull very low. In my opinion he makes it very much too flat. The reptilian eye is fairly spherical and the sclerotic plates show that it filled the orbit well. In Watson's restoration, it would be quite impossible to accommodate a spherical eye whose diameter was

about equal to the length of the orbit. Hence Watson's restoration of the temporal region must be in error. Either there was a deep continuous outer temporal wall, or there were two arches as in *Sphenodon*. Boulenger has recently reëxamined the skull of the allied *Saphæosaurus* and satisfied himself that it is undoubtedly a two-arched form, but he points out that it differs from *Sphenodon* in having both a supratemporal and squamosal.

The examination of the skull of *Youngina capensis* confirmed me in my opinion of the lizard temporal bones. In *Youngina* there is a large squamosal with a small quadratojugal below it and a small additional bone above. This upper bone, which I identify as the tabular, as I do the upper bone in the lizard, is the same as the bone which in *Saphæosaurus* Boulenger calls the supratemporal.

For further help I thought it might be well to study carefully the condition of affairs in the primitive, if very aberrant, *Chamæleon*.

In 1880 Kitchen Parker published an account of the structure of the *Chamæleon* skull. While showing the same care and marvelous minute dissection that characterizes all his papers, it unfortunately is marred by his having misunderstood the nature of the parietal region, and his great authority has led to the acceptance of his opinion by others. Methuen and Hewitt have corrected Parker's error.

In the genus *Chamæleon* as represented by *C. vulgaris* and *C. quilensis* we have a parietal which, from a transverse articulation with the frontal and small lateral articulation with the postorbitals, is produced backward as a narrow median crest. All this parietal was held by Parker to be the interparietal. The upper and posterior fourth of the orbital margin is formed by the large postorbital, which also sends a process backward to meet the squamosal and with it forms the temporal arch.

The bone which I hold with most others to be the squamosal is a triradiating bone. The anterior process, besides forming a long articulation with the postorbital, passes downward and meets the upper end of the jugal. The descending process, which is well developed, meets the upper end of the quadrate, while the lower end of the squamosal is supported by the paroccipital process. It is for the most part only indirectly so; as the little bone which I believe to be the tabular is wedged in between the two. There is, however, a small part of the squamosal that directly articulates with the paroccipital. The ascending branch of the squamosal passes right up to meet the parietal median crest almost in the middle line. In some specimens of *C. quilensis* they actually meet over

the top of the parietal, and this seems also to be the case in *C. dilepis*. Instances of squamosals approaching one another near the middle line are met with in many groups, such as Plesiosauria, Chelonia (e.g., *Hydromedusa*) and even Therapsida and Mammalia, but in no known groups do quadratojugals ever approach each other in the middle line. Yet this is the bone which is the undoubted homologue of the one in lizards that is held by Watson to be the quadratojugal.

The small bone which I call the tabular was well figured and described by Parker as the supratemporal. It is entirely on the occipital face of

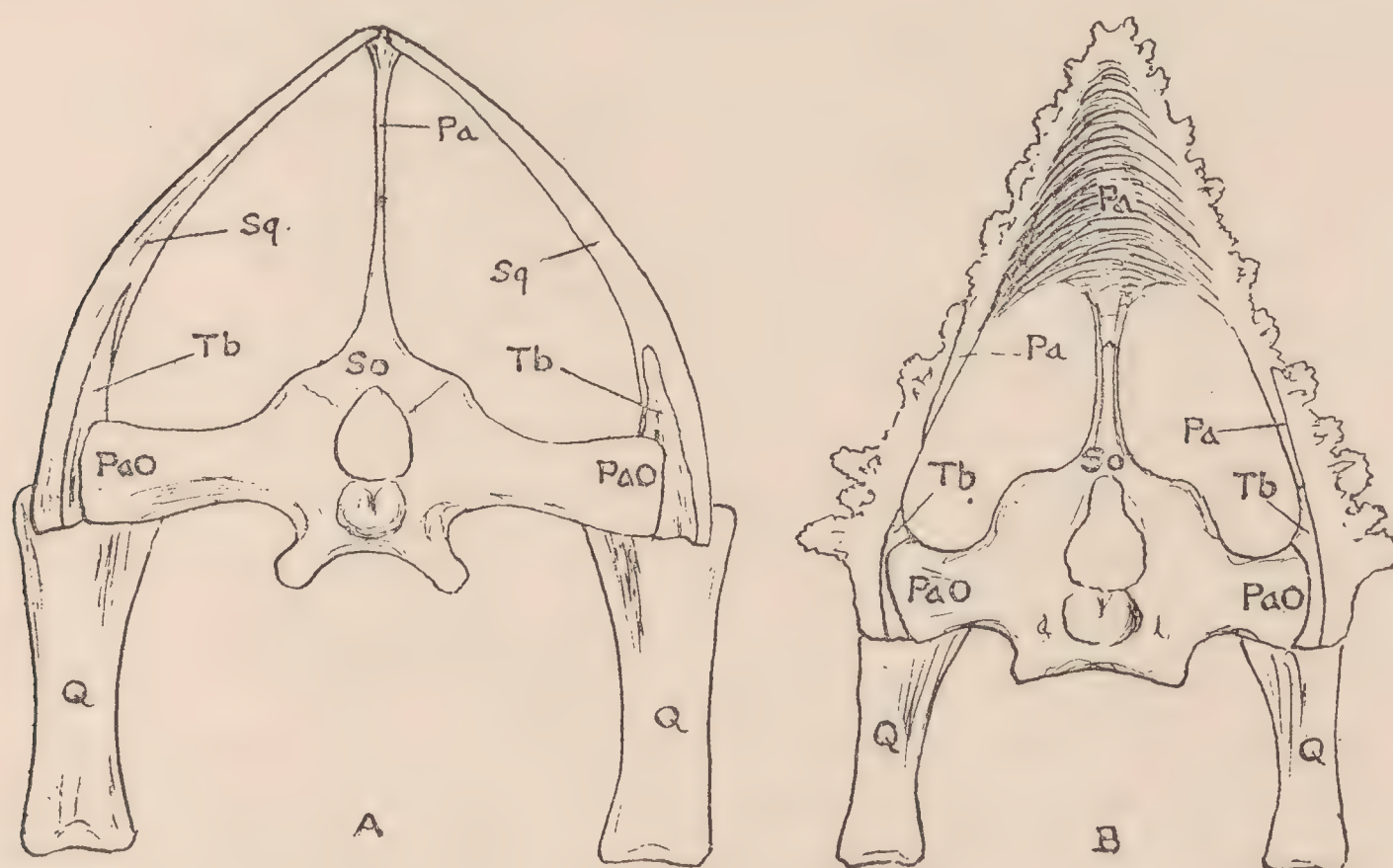


Fig. 1. A. Occiput of *Chamæleon quilensis*.¹

B. Occiput of *Lophosaura* sp., showing the relations of the tabulars to the neighboring bones.

the squamosal, with the lower part wedged between the squamosal and the paroccipital. It has a fairly large articulation with the quadrate. The upper end of the tabular reaches to the level of about the middle of the post-temporal arch.

The small chamæleons have a skull which differs so very greatly from the typical forms that they must be placed in a distinct genus, *Lophosaura* Gray. The typical chamæleons lay eggs; the species of the genus *Lophosaura* are viviparous. The most striking characters of the skull of *Lophosaura* are, that the parietal, instead of forming a narrow median crest, forms a fairly broad casque which sends down lateral

¹References to lettering in figures: A.C., Auditory capsule; Ang., Angular; Art., Articular; Bo., Basioccipital; Co., Coracoid; D, Dentary; D.M., Depressor mandibulæ muscle; E.O., Exoccipital; E.Pt., Epipterygoid; F., Fr., Frontal; Ip., Interparietal; Ju., Jugal; L., Lachrymal; M.C., Meckel's cartilage; Mx., Maxilla; Na., Nasal; Pa., Parietal; P.Art., Prearticular; Pa.O., Paroccipital; Pmx., Premaxilla; Po.F., Postfrontal; Po.O., Postorbital; Pr.F., Prefrontal; P.S., Parasphenoid; Pt., Pterygoid; Q., Quadrate; Q.J., Quadratojugal; S.Ang., Surangular; S.O., Supraoccipital; Sp., Splenial; Sq., Squamosal; Tb., Tabular; T.M., Temporal muscle.

processes to become part of the post-temporal arches; that the squamosals have only short ascending processes and merely form part of the post-temporal arches; and that the prefrontals and postorbitals do not meet above the orbits.

The squamosals do not meet the jugals as they do in *Chamæleon*, but in some species they approach pretty close to them. The descending process of the squamosal is so short that it can hardly be looked on as a process at all. It is almost entirely separated from the paroccipital by the interposed tabular. Only for a very small space in front does it touch. In *L. tæniabronchus* the squamosal forms the greater part of the post-temporal arch, meeting and passing to the back of the descending parietal process. In another species of which I have the skull, probably *L. damaranus*, the post-temporal arch is formed almost as much by the parietal as by the squamosal, the parietal forming most of the inner and anterior side by a long, slender descending process.

On one side of this skull the descending process of the parietal nearly meets the tabular and on the other it forms an articulation with it.

The tabular is considerably smaller relatively than in *Chamæleon* and is mainly packed in between the end of the paroccipital and the squamosal. It has a fairly strong articulation with the quadrate.

While the study of the condition in the adult skulls of *Chamæleon* and *Lophosaura* leaves in my mind no doubt that the large bone is the squamosal, some doubt might remain as to whether the small bone is the supratemporal or tabular. The large bone agrees very closely in its relations with the large bone which is believed to be the squamosal in *Sphenodon*. It articulates in front with the postorbital as in *Sphenodon*, it supports the quadrate, and it has an ascending process for articulation with the parietal. There is, further, no doubt that the bone regarded as squamosal in *Sphenodon* is the same as the bone which is called squamosal in the therapsids and which, unquestionably, is the homologue of the mammalian squamosal. That it cannot be the quadratojugal scarcely requires any argument.

The small bone, if the large one is, as seems certain, the squamosal, must be either a supratemporal, a tabular or a neomorph. As the evidence from the adult skull is not as convincing as one would wish, I have examined a number of early developmental stages of the skull of *Lophosaura*, and the relations of the bones when they commence to ossify is very suggestive.

Most of the membrane bones of the temporal region ossify at the same time, but the squamosal and the postorbital ossify a little earlier

than the parietal, the jugal or the tabular. But in an embryo very slightly larger than that which shows the first ossification of the squamosal, we find all the other membrane bones well ossified. The tabular is so early and so well ossified, though it is so small a bone in the adult, that we may safely assume that it is a primitive skull element and not a

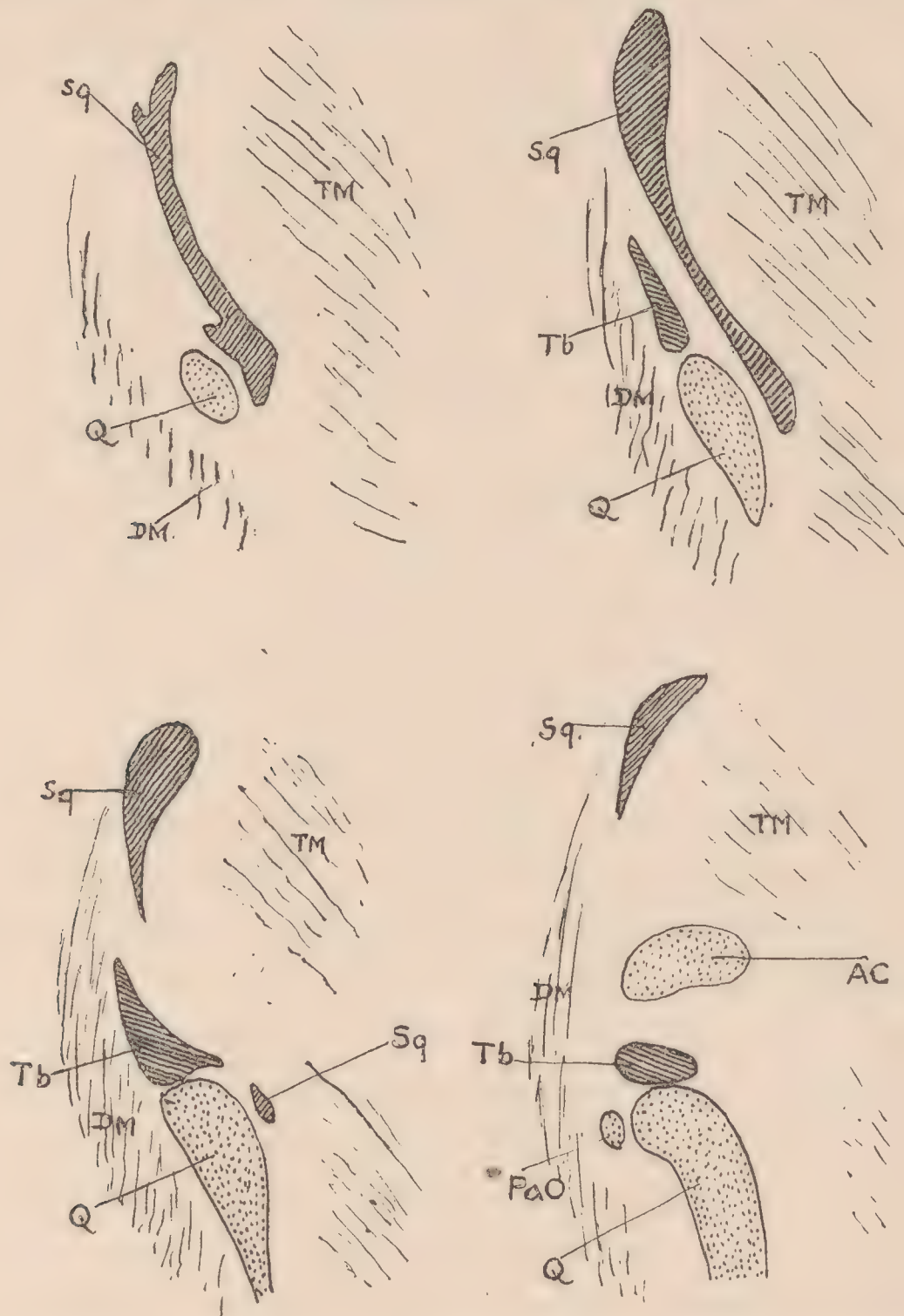


Fig. 2. Tangential sections (1, 4, 7, 10) through the upper end of the quadrate and associated bones of an early embryo of the chamæleon, *Lophosaura tæniabronchus* Smith, showing that, in this form, the supposed tabular is an occipital element practically excluded from the temporal fossa by the squamosal, and that it gives no attachment to any of the fibers of the temporal muscle, though giving attachment behind to part of the depressor mandibulæ.

neomorph. I have given a series of tangential sections of the quadrate region in an embryo *Lophosaura* of head length of 4.5 mm. The four sections given are all equidistant one from the other and may be numbered 1, 4, 7, 10. Section 1 is immediately outside the end of the tabular.

Section 4 shows the tabular supporting the quadrate and entirely behind the squamosal.

It will be observed that no fibers of the temporal muscle can approach the tabular, though, posteriorly, it gives an attachment to the muscle which pulls up the posterior angle of the jaw. Section 7 shows the relations of the muscles even more fully; and, though here the squamosal is no longer in front, there are no fibers of the temporal muscle near it. The next section, which is through the inner corner of the tabular, shows that, though the squamosal is no longer in front, a large part of the auditory capsule is seen in front, and, though the squamosal as ossified is not quite in contact with the paroccipital, we know that it is in contact in the adult and that there are certainly no muscular fibers passing between. So that, in reality, the tabular is practically shut out from the temporal fossa and is entirely a bone of the occiput.

The supratemporal is, really, in the stegocephalians and those cotylosaurs in which it occurs, a roofing bone of the temporal fossa which doubtless gave attachment to a portion of the temporal muscle. The tabular, though it is originally a bone of the top of the skull, in stegocephalians is largely an occipital element, and, in most early reptiles in which it is retained, purely an occipital element. Normally it is situated between the interparietal and parietal above and passes down between the paroccipital and the squamosal below. If the small bone in lizards is one of these two elements, as seems pretty certain, it appears to me that it must be regarded as the tabular.

Watson says, "In the great majority of Therapsids a tabular is present. In all cases it lies entirely behind the parietal and squamosal."

Having considered the question of the homology of the two bones and seen reasons for regarding the upper as the tabular and the outer bone the squamosal, let us consider whether we have good reason for holding that the lizards have lost the lower arch or whether Watson is right in regarding the lizard arch as representing both arches of *Sphenodon* and our supposed squamosal as the quadratojugal.

Many years ago I became convinced of the truth of that part of the recapitulation theory which holds that developing embryos frequently retain ancestral characters which are lost in the adults; and, in dozens of embryos of reptiles, birds and mammals that I sectioned in my hunt for such ancestral features, a good many startling discoveries were made. I found that the early marsupial has a monotreme-like coracoid which articulates with the sternum; that the ostrich embryo has four digits in the manus and five in the pes, and that the human foetus has the central

carpal element. I examined the lizard embryo to see if there were any evidence of a fixed quadrate and found that there was very distinct evidence thereof.

As the paper in which I described my results has been lost sight of, I think it may be well to reproduce some of the figures, which are very striking. I could discover no trace of a quadratojugal bone, but I found

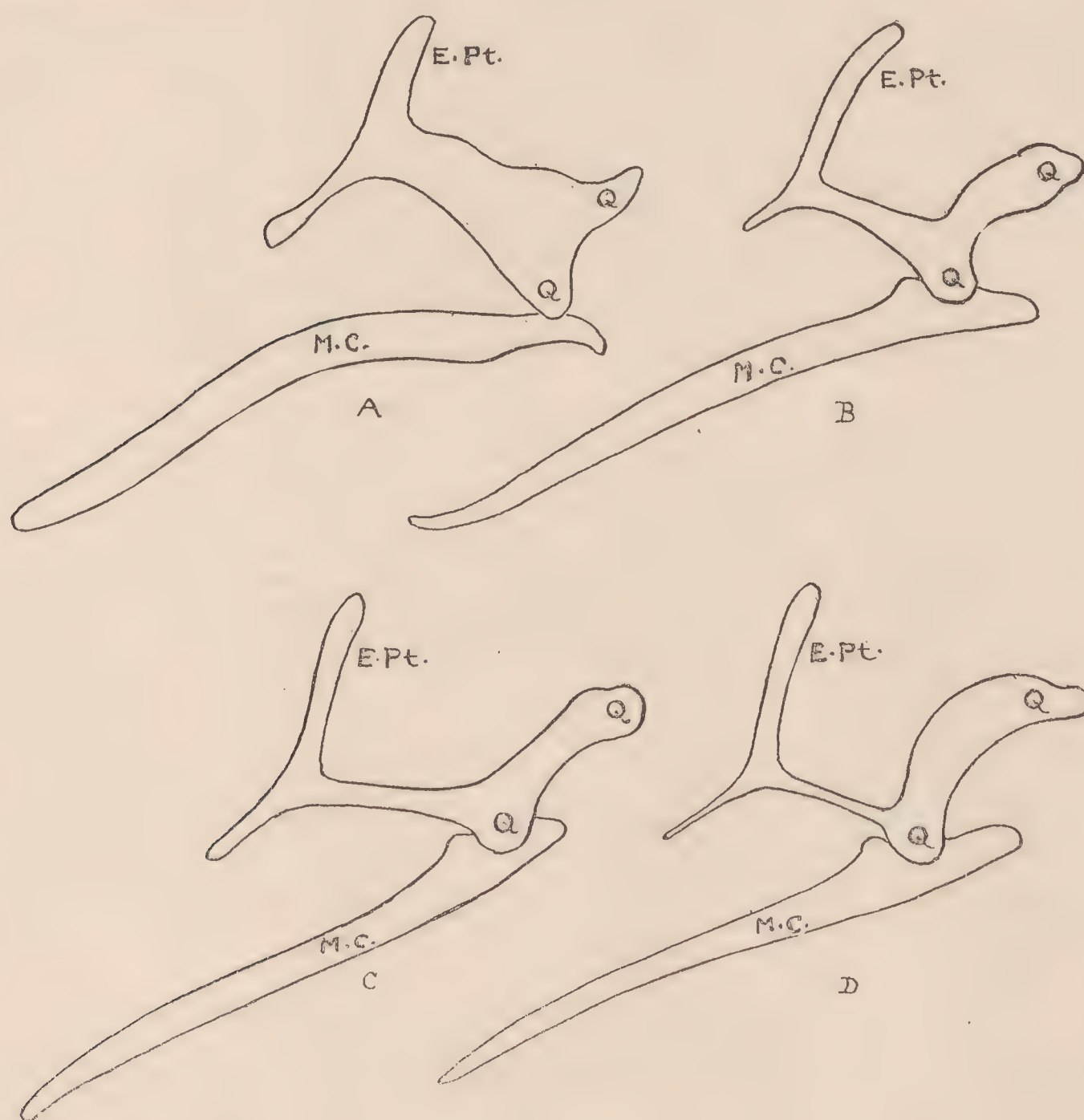


Fig. 3. The lower jaws with quadrate, epipterygoid and connecting cartilaginous bar in embryos of A, *Sphenodon punctatus* Grey (after Howes and Swinnerton); B, *Eremias capensis* Smith; C, *Zonurus polygonus* Smith; D, *Mabuia sulcata* Peters; showing that lizard embryos have a fixed quadrate almost exactly as in *Sphenodon*.

in such different lizards as *Zonurus*, *Eremias* and *Mabuia* a well-developed cartilaginous bar fixing the lower end of the quadrate to the lower end of the epipterygoid almost exactly as in *Sphenodon*, and in *Agama* and *Lophosaura* distinct remains of the bar, though here it is no longer chondrified. The resemblance to *Sphenodon* is so close that we can safely homologize regions, and as in *Sphenodon*, the small quadratojugal is situated at the lower end of the quadrate. We may be certain that the

ancestral lizard quadratojugal was also in this region. In *Youngina* the quadratojugal is also low down in a line with the jugal. The quadratojugal ligament is doubtless the remains of the lower arch in the lizard. If a bony arch is replaced by a ligamentous one, the bones that formed the arch can cease to be ossified, but they cannot wander away.

DERIVATION OF THE LIZARDS

There is nothing in the girdles or feet that does not support the view that the lizards are derived from a form near the ancestor of *Sphenodon*, but from a form which still retained the two bones in the temporal region. *Sauranodon*, *Pleurosaurus* and *Saphæosaurus* give us some indications of what the ancestral condition of the temporal region was like. *Sphenodon* may be regarded as a primitive lizard which still retains the quadratojugal but has lost the tabular, or, as Boulenger would prefer to call it, the supratemporal.

There is one other probably allied group to which reference may be made,—the Thalattosauria of Merriam. Unfortunately, the group is not so well known as one would desire, and no known specimen has the temporal region perfect. If Merriam's restoration of the top of the skull be compared with Lortet's figure of *Sauranodon* or Watson's of *Pleurosaurus*, it will be observed that there is a very considerable resemblance between them, and that all that is missing from the upper part of the temporal region is the tabular. When the tabular is restored, it will be seen that the Thalattosauria are aquatic forms closely allied to the land animals from which branched off the lizard *Sphenodon* and the Sauranodontidæ.

RELATIONSHIPS OF THE CHELONIA

The second group of reptiles which has given rise to trouble is the Chelonia, and there is no order of reptiles living or extinct concerning whose affinities greater differences of opinion have been expressed. Had the order been extinct, known only by imperfect specimens, one could easily have understood the uncertainty, but it is an order represented by very many living species inhabiting most parts of the world. The anatomy of typical examples is as well known as that of the frog, and thanks to the lamented Mitsukuri, the embryology is as completely known as that of almost any living vertebrate.

Unfortunately, the members of the order are all extremely specialized and in some respects degenerate, so that the picking out of the ancestral characters amid the more recent specializations is somewhat like the reading of a difficult palimpsest.

The principal views that have been expressed are: (1) that the chelonians are allied to the rhynchocephalians; (2) that the nearest allied forms are the plesiosaurs; (3) that they are allied to the anmodonts, and (4) that they are modified cotylosaurs.

It will be unnecessary to discuss at any length these various views, nor would it be possible for me to do so fully or satisfactorily, writing as I am seven hundred miles from the nearest scientific library. Watson, in his recent paper "*Eunotosaurus africanus* Seeley and the Ancestry of the Chelonia,"¹ has dealt at considerable length with what he considers to have been the characters of the hypothetical ancestor "Archichelone." He considers the skull to have been a completely roofed skull such as is seen in the Cotylosauria and that the girdles were of the "old-fashioned" type,—the shoulder girdle having the primitive two coracoidal elements and the pelvis a plate-like pubis and ischium. Were this so, there could be little doubt that the chelonians sprang directly from some cotylosaurian ancestor and that they are not nearly related to any of the later reptiles. The limbs he also holds are such as might readily be derived from a cotylosaurian type. Versluys had previously, though very guardedly, expressed the opinion that the ancestor of the Chelonia may have been a cotylosaur, and Williston had made the same suggestion as early as 1907.

Watson obtains considerable support for his view from the remarkable South African fossil reptile *Eunotosaurus*. This imperfectly known animal has eight greatly developed broad ribs, which certainly have a considerable resemblance to a chelonian carapace, and the shoulder girdle and pelvis are apparently of the primitive type. He concludes that "so far as the structure is known, *Eunotosaurus* agrees exactly with the hypothetical 'Archichelone'" and that "it is by no means improbable that it is an actual ancestor of the Chelonia." He adds "whether it be or not it does, I think, give us a great many suggestions of the changes which must have taken place during the development of the Chelonian shell and all that it implies."

Eunotosaurus is unfortunately imperfectly known. We know very little of the skull, only a little of the girdles and nothing of the manus and pes. We do not know whether the skull is roofed, and certainly the vertebræ so far as known differ greatly from those of any known cotylosaur. The large ribs do not meet to form any sort of carapace but really overlap and are apparently freely movable. The specimen (B. M. 4054) figured by Watson is, apparently, not much crushed, and it seems to

¹1914. Proc. Zool. Soc., p. 1011.

show that the body of the animal was deeper than broad, and, as the limbs so far as known are relatively very feeble, we seem forced to the conclusion that the animal must have been an aquatic form. But, till a really good specimen of *Eunotosaurus* is discovered, it will be quite impossible to form any definite conclusions as to its affinities.

The chelonian is manifestly an extremely aberrant type, where the ancestral characters are so obscured by their being intermingled with remarkable specializations that it is very difficult to tell which is which, and our idea of the structure of "Archichelone" will entirely depend on which characters we regard as primitive. Those who regard the structure of the temporal region of the skull as the safest guide to affinity will naturally place the chelonians either with the primitive mammal-like reptiles or the cotylosaurs; those who hold that more reliance can be placed on the structure of the girdles and limbs will be more impressed with the affinities to the primitive diapsids such as *Sphenodon*.

Cope, Smith Woodward, Osborn and others have shown how extremely important the structure of the temporal region is as a guide to classification. In the mammal-like reptiles we have a temporal arch formed by the squamosal and jugal which scarcely shows any alteration in structure from the pelycosaurs to such varied groups as the dinocerophalians, the anmodonts, the dromasaurians, the therocephalians, the gorgonopsians, the cynodonts and even on to the mammals. Then again we have a large number of reptilian orders in which we find with little variation two temporal arches,—an upper postorbito-squamosal and a lower quadratojugo-jugal arch. All reptiles whose arches conform to one of these two types we can place with such confidence that there is rarely any difference of opinion. But all those whose arches are anomalous have given rise to the greatest difference of opinion,—lizards, snakes, placodonts, plesiosaurs, ichthyosaurs and chelonians.

While everyone must agree to the extreme importance to be placed on the structure of the temporal arches, it must be admitted, nevertheless, that we do occasionally find most remarkable variations in the structure in even allied forms. We have merely to look at the different suborders or families of the Lacertilia to see how unreliable the structure of the temporal region may become as a guide to classification.

Let us look at three well-marked common lacertilian types such as are lying before me,—a varanid, *Varanus*, an agamid, *Chlamydosaurus*, and a scincid, *Cyclodus*. All will agree that they belong to the Lacertilia, but the arches differ considerably. In the agamid, there is a powerful postorbital arch formed by the jugal and the postorbital, and a large

supratemporal fossa bounded mainly by the parietal and the postorbital. In the varanid, the jugal is rudimentary and there is no complete postorbital arch, but the supratemporal fossa is bounded essentially as in the agamid. In the scincid, there is a postorbital arch formed mainly by the jugal, but when we look for the supratemporal fossa, we find the top of the skull completely roofed. There is a broad parietal which, laterally, meets the long postorbital and, more posteriorly, the bone which I regard as the squamosal. Here there can be no doubt that the upper temporal fossa has become lost by the parietal and the postorbital coming together.

In other lacertilian types we can see the intermediate stages. If Watson be right that the lacertilian ancestor never had an infratemporal fossa and that the lateral broad bony arch became emarginated from below, then the scincid skull is as much a completely roofed skull as that of the chelonian, and there is exactly the same amount of evidence in favor of the scincid's being descended directly from a cotylosaurian ancestor as there is in the case of the chelonian, and, curiously enough, exactly the same bones form the roof,—a broad parietal with, laterally, the postorbital and the squamosal. Yet we know beyond all doubt that the scincid is not a direct descendant of a cotylosaur; and thus we see how very misleading the condition of the temporal region may become.

It is only a very few chelonians that have a roofed skull at all. The large majority have an open temporal region. And, if it by no means follows that a roofed temporal region indicates a cotylosaurian ancestry, then there is not a single other scrap of evidence pointing to such affinity, while I hold that there is the very strongest evidence pointing to a quite different ancestry.

Apart from the development of the carapace and plastron, the most remarkable feature of the chelonian structure is the peculiar shoulder girdle. This consists of a long rod-like scapula from whose lower end there passes inward a long rod-like prescapular process and a long slender coracoid. It has been suggested by various authorities that the prescapular process is a precoracoid, but there is not the least doubt that, as held by Baur, it is a true scapular development, and that there are only two cartilage-bone elements in the girdle, the scapula and the coracoid. An anterior scapular development of this sort is met with in only a very few forms, such as the plesiosaurs and the ostrich, and it is evidently a provision of nature for a large ventral muscular attachment, where one of the original coracoidal elements is lost. It could not occur in any form where both coracoid and precoracoid were present, and it is, to me, conclusive proof that the chelonian is not nearly related to the therapsids

but is descended from a lizard-like ancestor which had already lost one of the coracoidal elements.

The pelvis and the tarsus are very like those of *Sphenodon*, and Goodrich considers that the similar specialization of the fifth metatarsal in the two types is evidence of a close affinity, apparently implying that the common ancestor had this character. Though I agree with Goodrich that the Chelonia are much more nearly related to *Sphenodon* than to the mammal-like reptiles or even to the cotylosaurs, I do not consider that the common ancestor had either an open pelvis or a hooked fifth metatarsal. Most early rhynchocephaloid reptiles have a plate-like pelvis, and the earliest known form, *Youngina*, has not only a plate-like pelvis but also a moderately straight, unhooked fifth metatarsal, and it even retains the fifth distal tarsal.

It is much to be regretted that we do not know the skull of *Protorosaurus* thoroughly. There is some reason to believe, however, that it has only a single supratemporal fossa, and, if this be so, it must be pretty near to the lizard-like forms with the single upper opening, from which I believe the Chelonia must have sprung. It is held by Goodrich to have a hooked fifth metatarsal, and there seems to be evidence of a plate-like pelvis opening up. If *Protorosaurus* has only a single temporal opening, and thus is near the chelonian ancestor, then the evidence will be fairly strong in favor of both the hooked fifth metatarsal and the lizard-like pelvis of the Chelonia and the Rhynchocephalia having been independently formed by convergence. And, further, if the lizards and *Sphenodon* are both derived from a *Youngina*-like form, then the striking resemblance in the pelvis and tarsus of these must also have been due to convergence.

It would appear as if any Permian or Triassic reptile with the primitive plate-like pelvis and simple tarsus which took on a lizard-like habit developed independently—apart altogether from the structure of the skull—an open pelvis and a hooked fifth metatarsal. In the light of the paleontological evidence, it is much easier to believe this than that all forms with a hooked fifth metatarsal inherited this from a common ancestor which had this character. If we try to accept this latter view of Goodrich, our difficulties are overwhelming in connection with primitive two-arched forms such as *Youngina*, which is a typical diapsid or sauropsid, yet has not the hooked fifth metatarsal. We cannot admit the possibility of *Youngina*, like most dinosaurs, having lost the character, for the retention of the fifth distal tarsal renders it certain that no ancestor of *Youngina* could ever have had a hooked fifth metatarsal.

All the evidence at present available from comparative anatomy, embryology and paleontology seems to me to point to the chelonians having arisen from an Upper Permian or Lower Triassic somewhat lizard-like reptile which had a skull not unlike that of *Sphenodon*, but with only a supratemporal fossa, a shoulder girdle of the *Sphenodon* type, a plate-like pelvis and an unspecialized fifth metatarsal. Before any chelonian-like specialization took place, a more lizard-like habitus gave rise to a *Sphenodon*-like pelvis and a specialized hook-like fifth metatarsal.

Beyond this point we have no clear light to guide us, but possibly what happened was that the lizard-like ancestor became a semiaquatic, swamp-and-mud-frequenting animal, and, as a result of this change in habit, the body became broad and flat, and protecting dermal ossifications arose. The feeding on soft succulent plants and weeds led to the loss of the teeth and the development of a horny beak. The great development of the temporal muscle for the wide-snapping jaw led to the loss of the post-temporal arch in most types, though in some chelonians (e. g., *Hydromedusa*) this is still retained. The large majority of chelonians are still fresh-water-and-swamp-frequenting animals. Only a few have become dry-land forms, while others are pelagic.

RELATIONSHIPS OF THE PLACODONTIA

There is another group of reptiles which has caused some difficulty, namely, the Placodontia. As, however, we know little of the skeleton except the skull, few have ventured any very definite opinion as to their affinity. In 1861, Owen referred them to the Sauropterygia, but, in later life, thought the affinities were rather with the Anomodontia. Seeley definitely regarded the Placodontia as a suborder of the Anomodontia. Lydekker regarded the ordinal position as quite uncertain. Osborn, in his 1903 classification, followed Seeley's view.

More recently there has been a tendency to revert to Owen's early opinion and place the placodonts somewhere near the sauropterygians. Until we know something of the postcranial skeleton, the problem will remain in doubt, but there are two groups with which the skull seems to show more affinity. At first sight, the skull looks very unlike that of a chelonian, but, on more careful examination, there are seen to be some striking resemblances. The placodontian palate is a very remarkable type. The pterygoids are large flat bones which are firmly sutured to each other in the middle line and from the roof of the mouth to near the back of the skull. Laterally, they are firmly articulated with the large quadrates. This very unusual condition is found

elsewhere only among the chelonians and sauropterygians. The occiput of a placodont such as *Placochelys* is fundamentally so surprisingly similar to that of the chelonian that one is forced to the conclusion that the two types are closely related. For, while the occiput is almost chelonian in type, it is unlike that of any other reptiles except that

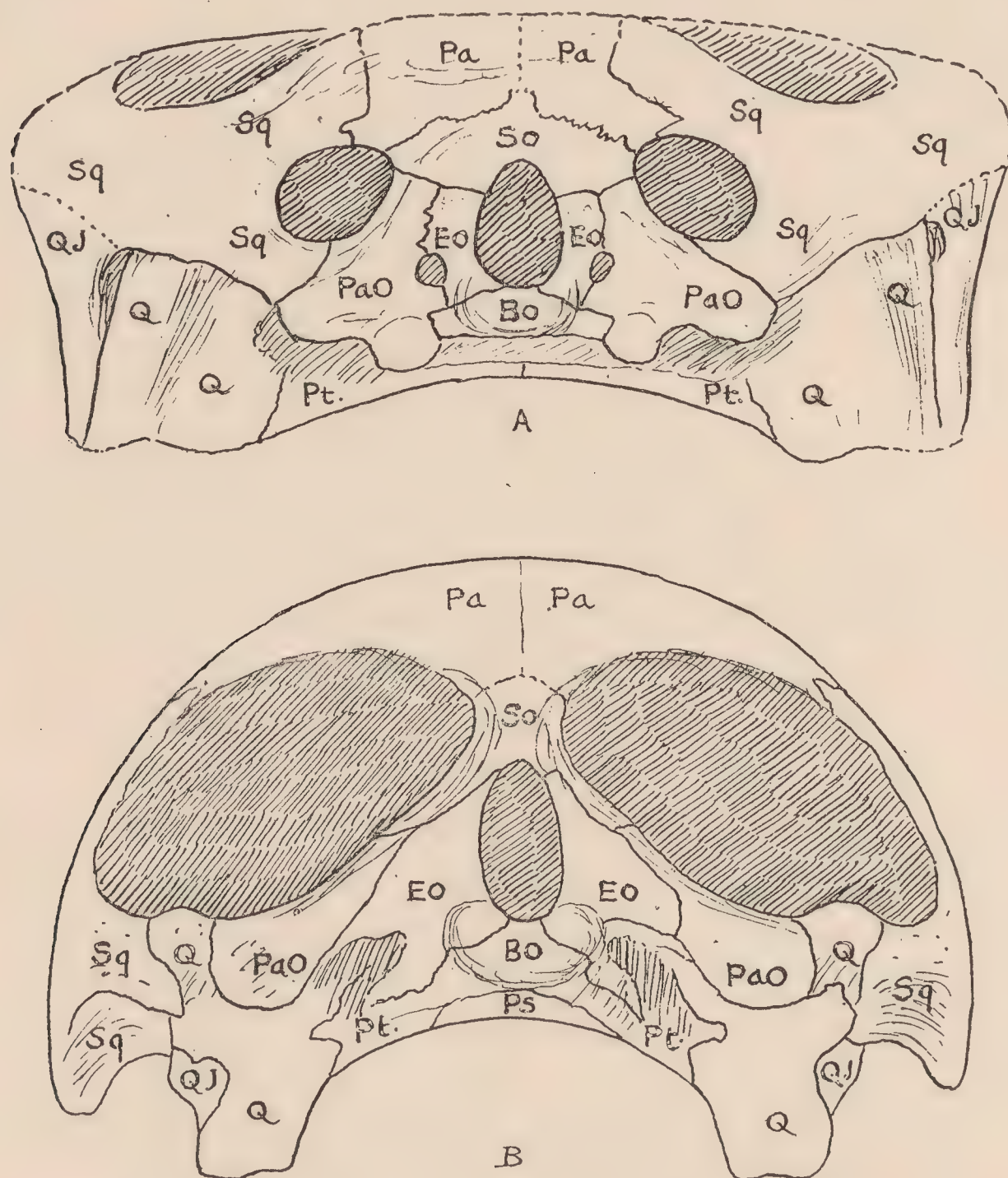


Fig. 4. A. Occiput of *Placochelys placodonta* Jaekel. After Jaekel, with the dermal ossifications omitted.

B. Occiput of *Dermochelys coriacea* Linn. After Nick.

A comparison of the two shows that the types are essentially similar, the chelonian differing from the placodont only in having lost the post-temporal arch, and in sometimes having, as in *Dermochelys*, the temporal fossa secondarily roofed by a posterior extension of the postorbital arch.

of the plesiosaurs and ichthyosaurs, with which it has some affinity, though more remote than with the chelonian. If we compare the side view of the skull of *Placochelys* with that of a chelonian like *Emys*, we again see the striking resemblance.

Of course there are the two great differences which have prevented the affinity from being generally recognized,—the presence of teeth and of a post-temporal arch in the placodont. But some ancestor of the Chelonia must have had teeth, and there is good reason to believe that the early chelonians also had a post-temporal arch. If this be so, then the placodonts may be merely highly specialized proto-chelonians, and the discovery of a very chelonian-like carapace in *Placochelys* strongly confirms this view.¹

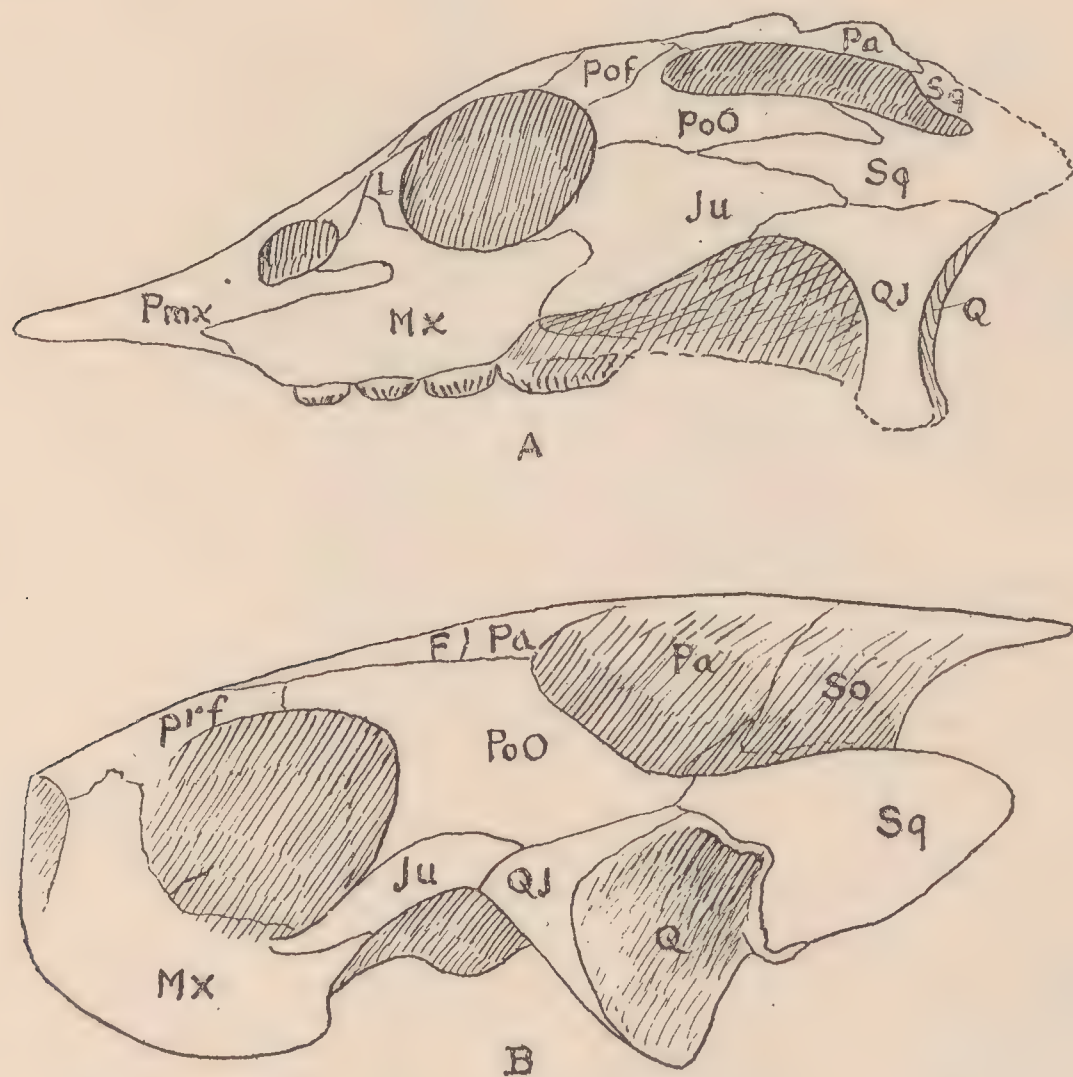


Fig. 5. A. Skull of *Placochelys placodonta* Jaekel. After Jaekel, with the dermal ossifications omitted.

B. Skull of *Emys orbicularis* Linn. After Rabl. Showing the similarity in the structure of the jugal arch in the two types.

RELATIONSHIPS OF THE PLESIOSAURIA

One other group which has given rise to much difference of opinion is the Plesiosauria. Andrews has recently summarized the principal different views that have been expressed, as follows:

Many writers (e.g., Baur and Fürbringer) have considered that there is a close relationship with the Chelonia, but the many objections to this view which have been summed up by Williston and Hay render it untenable. Broom considers that the group sprang from a land ancestor somewhat resembling *Sphenodon*, but with the supra-

¹Or, in other words, the chelonians may be regarded as the descendants of a placodont-like type which became edentulous and ultimately lost the post-temporal arch.

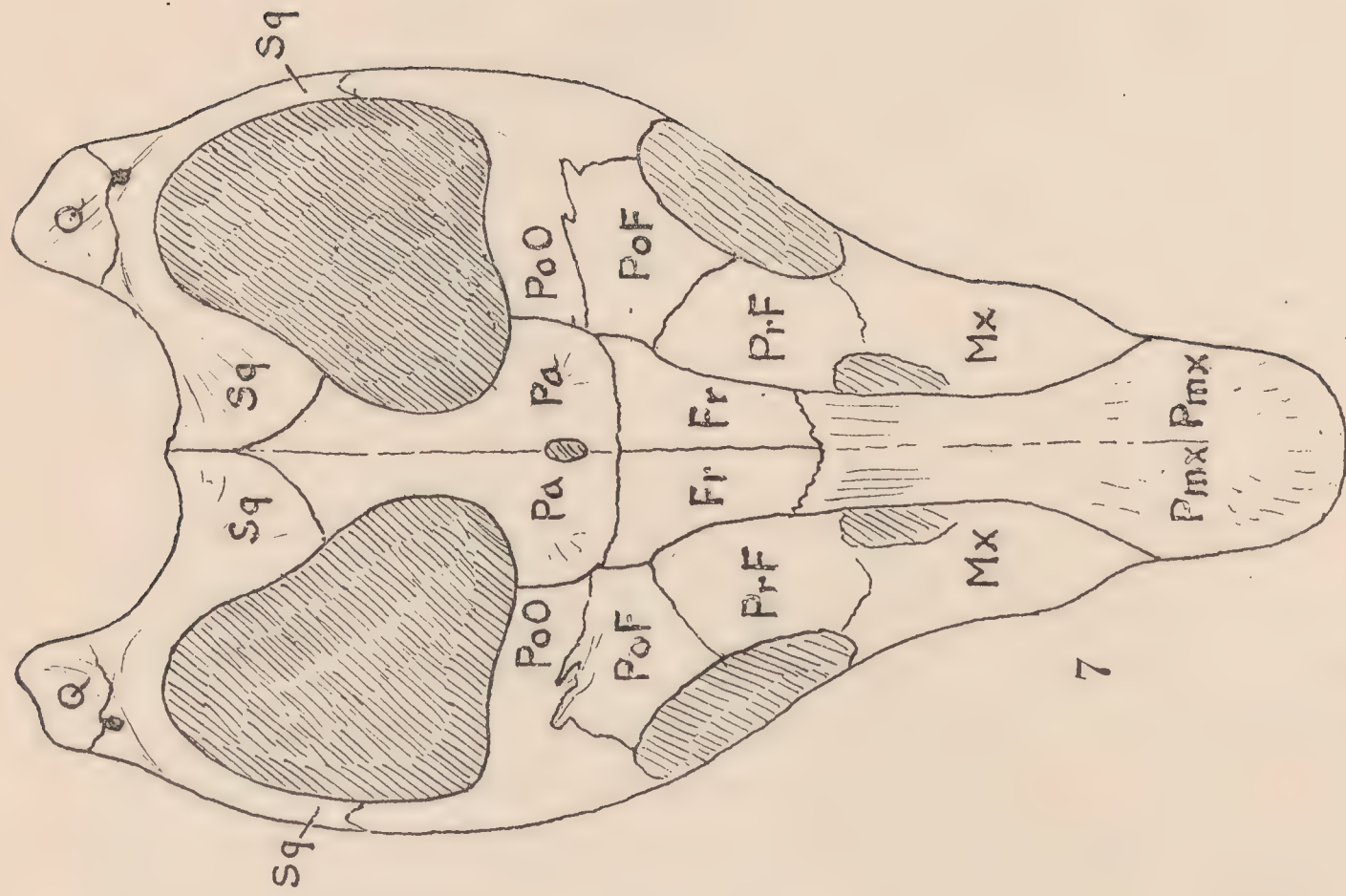


Fig. 6. Skull of *Placodus gigas* Agassiz. From a specimen in the British Museum. The sutures in line are those that I believe can be traced in the specimen.

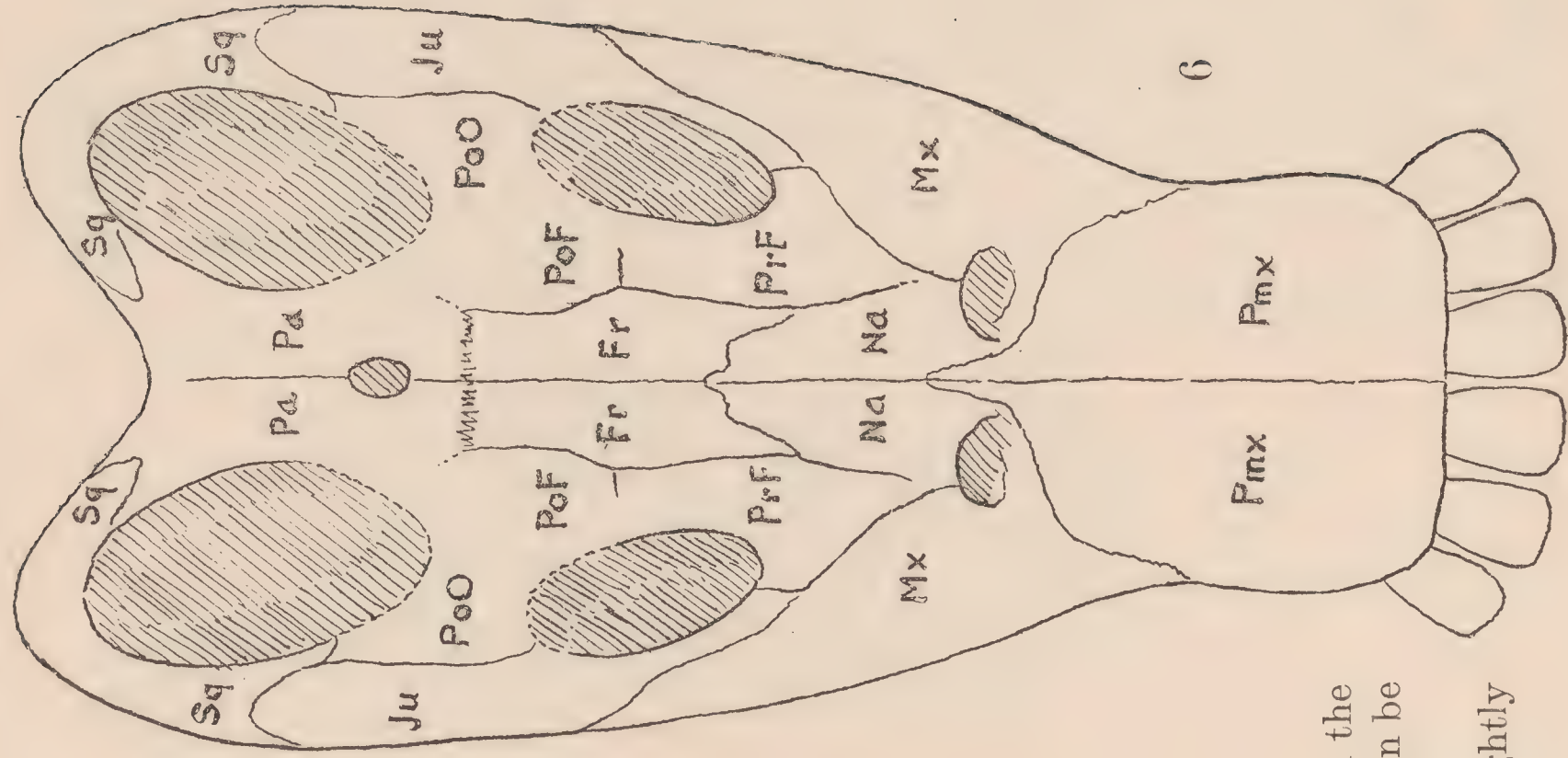


Fig. 7. Skull of *Plesiosaurus macrocephalus* Buckland. Slightly restored from the very fine skull in the British Museum.

témporal fossa alone developed; Jaekel, on the other hand, considers that both fossæ were developed, but that the lower temporal bar had been lost. The present writer [Andrews] also, chiefly on account of the structure of the palate, once regarded the Sauropterygia as descended from a primitive Rhynchocephalian reptile. Boulenger considers, as Seeley did, that *Mesosaurus* is closely related to the Sauropterygia; but the skull in *Mesosaurus* is too imperfectly known to be certain of its relationships

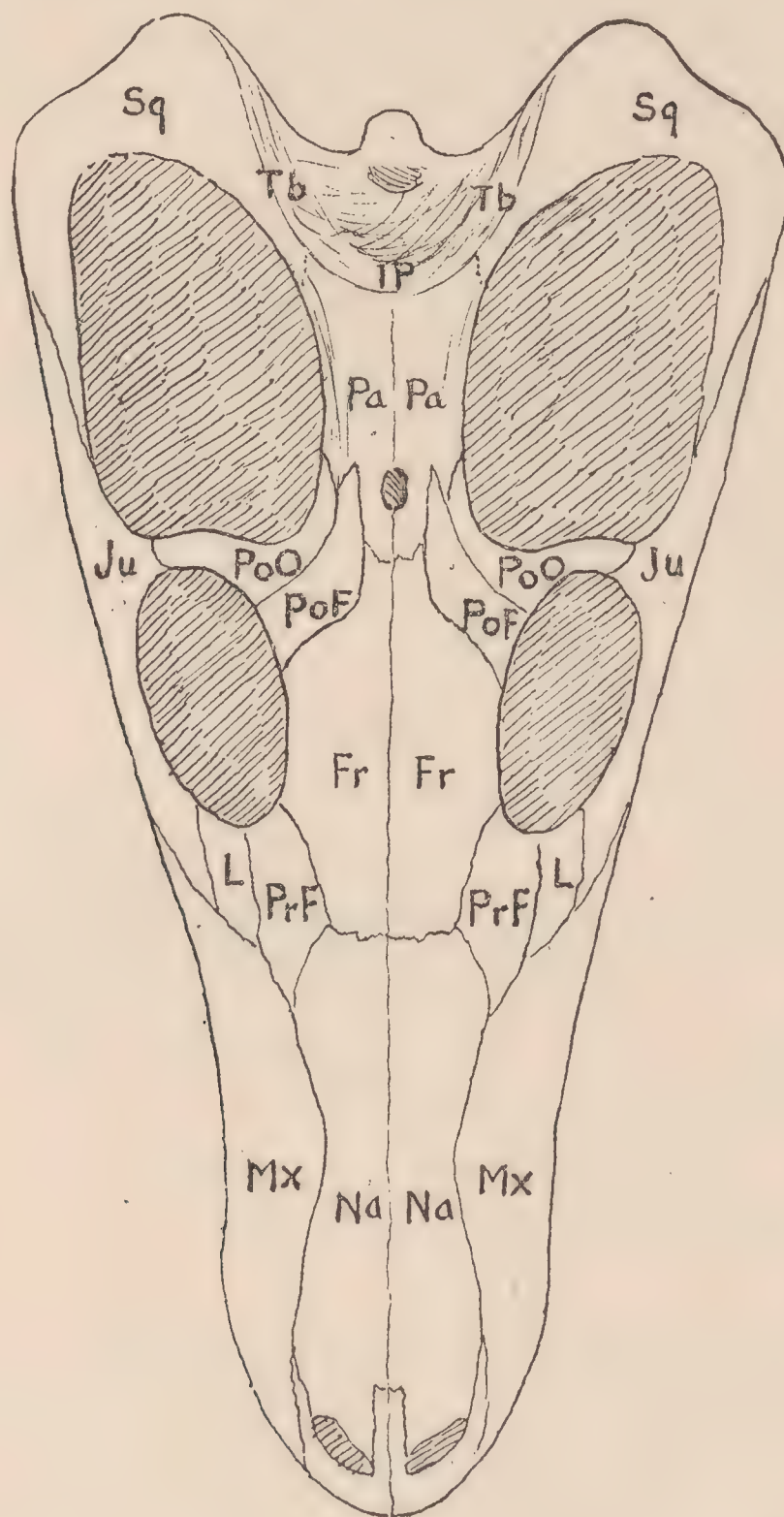


Fig. 8. Skull of a therocephalian, *Scylacosaurus sclateri* Broom, for comparison with the plesiosaurian skull.

either to the Sauropterygia or any other order, though it has been referred by Osborn to the Diaptosauria, a group including the primitive Rhynchocephalian types. A. S. Woodward and Williston, especially the last-named author, consider the group as nearly related to the Theriodontia.

Andrews discusses at considerable length the characters probably found in the ancestral plesiosaurian and concludes that it was related to the Dromasauria or to the primitive therocephalians.

The view which I expressed fifteen years ago, I have never seen any reason to change, and I am to-day more convinced than ever that it is correct.

The plesiosaurian skull is thoroughly well known, though only a very few good specimens have been discovered. The specimen which best shows the structure of the upper side is the skull of *Plesiosaurus macrocephalus*, figured many years ago by Andrews, and of which I give two new drawings differing in a few very minor points from that given by

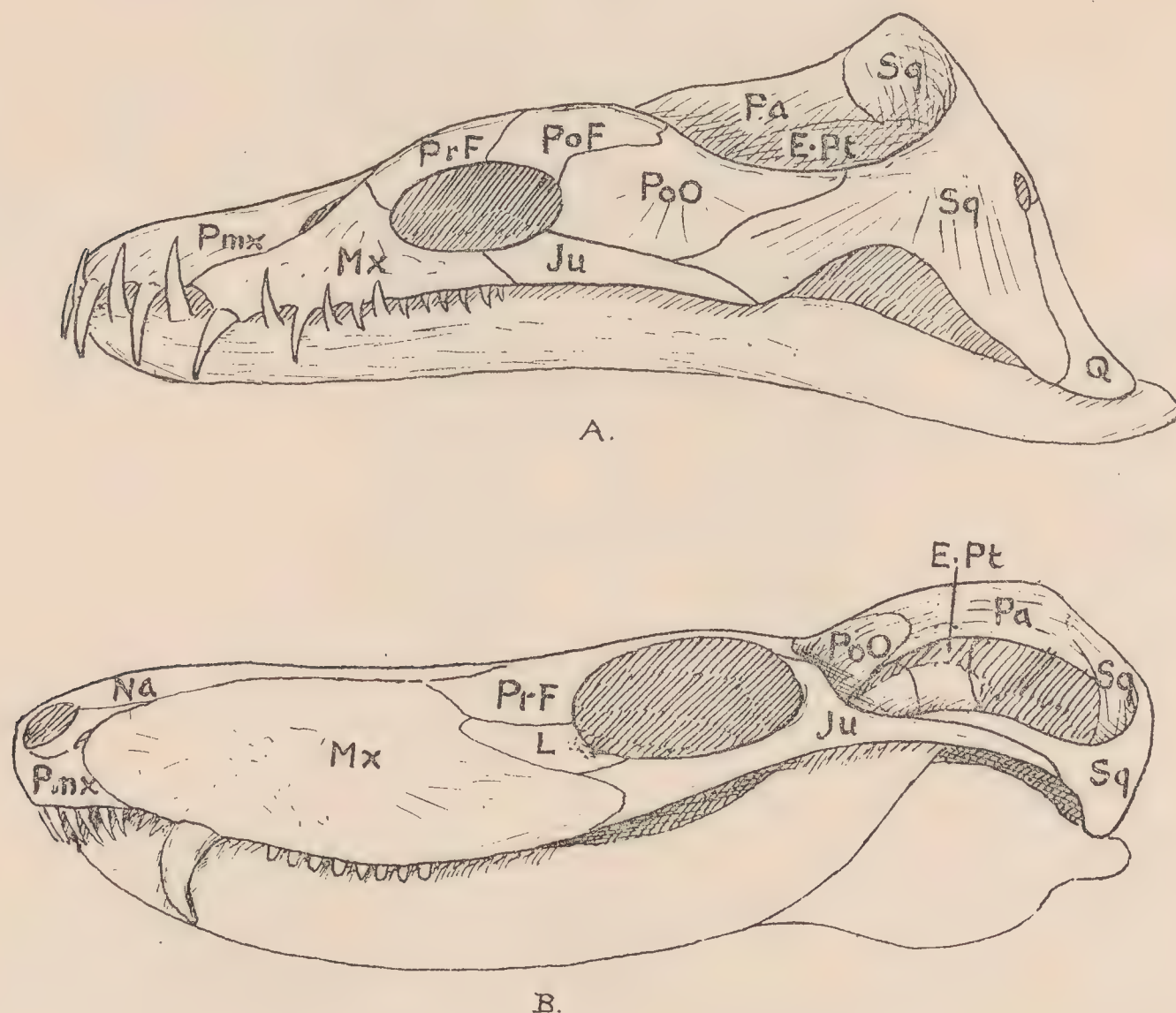


Fig. 9. Skull of *Plesiosaurus macrocephalus* Buckland, A, and skull of *Ictidosuchus longiceps* Broom, B, to show the resemblances and differences between the skull of a plesiosaur and that of a primitive therocephalian. The figure of the plesiosaur skull is slightly restored from the very fine skull in the British Museum; the figure of the *Ictidosuchus* skull is slightly restored from the type specimen.

him. Apart from the specializations seen in the plesiosaurian, it must be admitted that the general resemblance to the therocephalian skull shown is considerable. In each there is a single temporal fossa which, in the former, is bounded by the postorbital, the squamosal and the parietal, and, in the latter, by the postorbital, the jugal, the squamosal and the parietal.

Are the fossæ, however, really homologous? If the therocephalian skull and those of allied forms were unknown, I do not think anyone would

for a moment hesitate in concluding that the fossa in the plesiosaurian is the homologue of the upper fossa of the typical diapsidans. Yet we know from the position of the bones in allied groups that the fossa in the Therocephalia is originally a lower fossa which gradually encroached on the postorbital and squamosal above till it has reached the parietal and looks almost like a union of both the diapsidan fossæ.

But, apart from the resemblance of the fossæ, which I believe to be secondary, and primitive characters, such as the rhynchocephaloid structure of the palate, the two skulls do not greatly resemble each other, and in one or two points differ very fundamentally.

The plesiosaurian occiput is very unlike that of any therapsidan or even of the more primitive American pelycosaurs,—so very unlike that it is difficult even to compare them. Yet it resembles very considerably those of primitive diapsidans.

The mandible has been described by Andrews from a number of good specimens, but one or two new drawings will not be superfluous, considering the importance of the subject, and also as I have been able to discover a prearticular in both *Peloneustes* and *Plesiosaurus* which Andrews had not observed. In all specimens in which the back part of the inner side of the mandible is well preserved, a small prearticular can be seen in the situation indicated in the figures.

The plesiosaurian mandible will be seen to have very little resemblance to that of the therocephalians, though it has undoubtedly some considerable likeness to that of the dinocephalians and pelycosaurs, but not more than it has to that of primitive diapsidans.

The vertebræ and ribs in the plesiosaur are very unlike those of any therapsidans, but considering the great specializations in the former for an aquatic life, one can hardly expect much evidence of affinity from the vertebræ.

When we come to consider the structure of the girdles and limbs, we get evidence of a very clear and positive nature.

The shoulder girdle is fully known in a large number of genera. It consists of a very large coracoid which meets its neighbor in a large median suture, and a curiously twisted scapula which has a short upward and outward process and a large anterior and inward-passing process which, in many genera, also meets its neighbor in the middle line. Fundamentally, the shoulder girdle is strikingly similar to that of the chelonian and it seems probable that the two have a common origin. The type is known in no other reptiles, living or extinct.

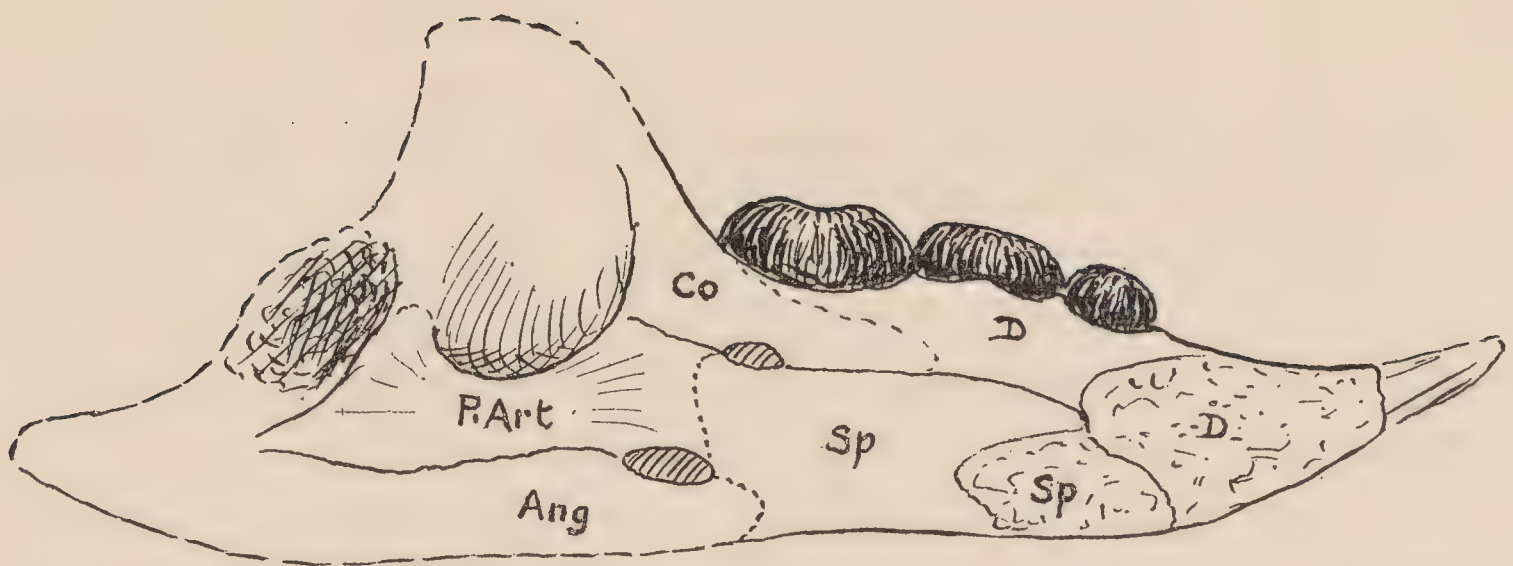


Fig. 10. Inner side of mandible of *Placodus* sp. Much reduced. Slightly restored from specimen in British Museum.

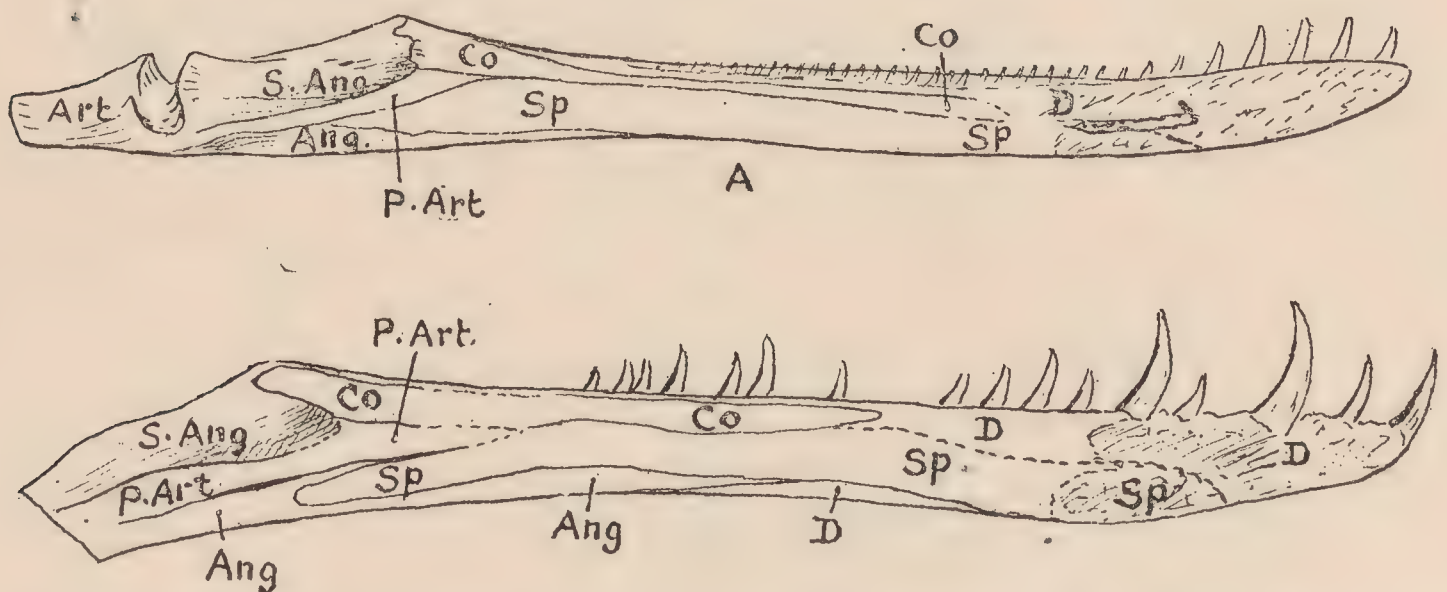


Fig. 11. A. Jaw of *Peloneustes philarchus* Seeley, B. M. 3803. Inner side. Reduced.

B. Imperfect lower jaw of *Plesiosaurus rostratus*, B. M. 38525. Inner side. Reduced.

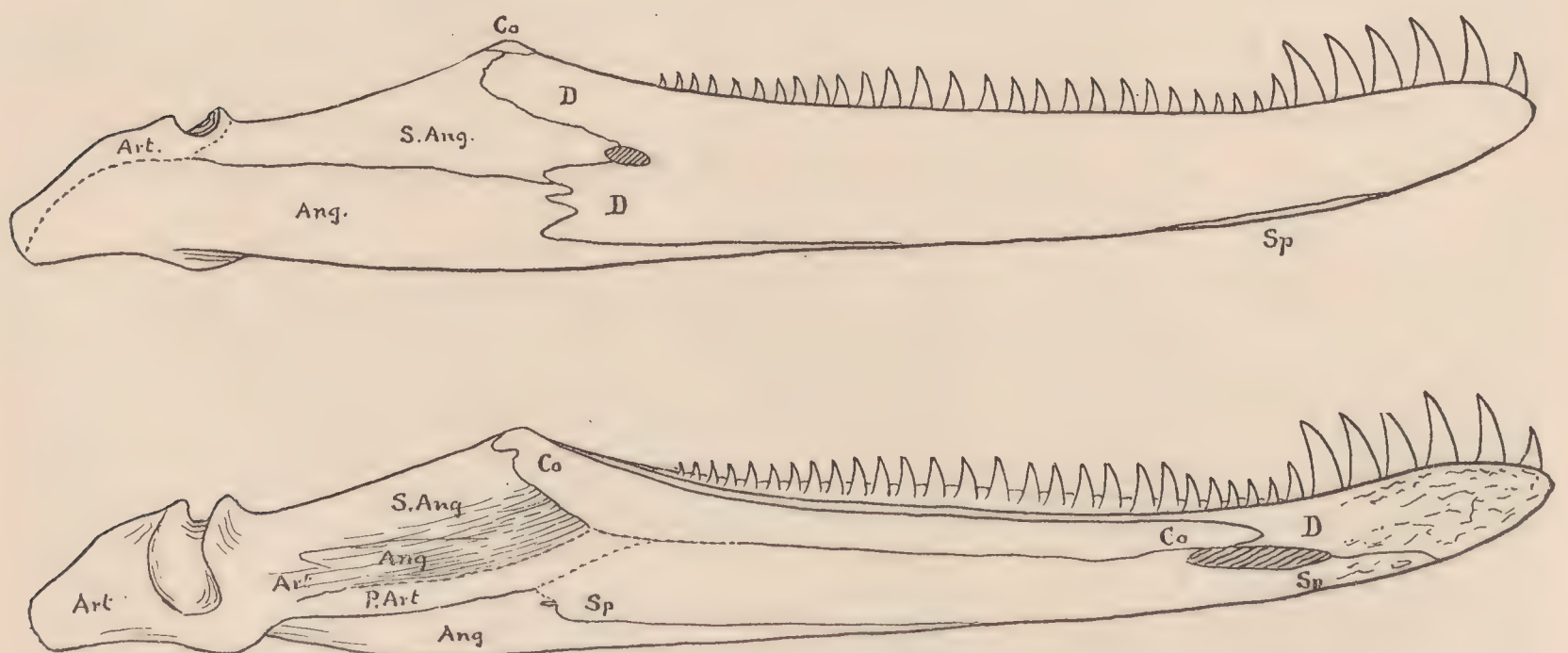


Fig. 12. Lower jaw of *Peloneustes evansi* Seeley.

In the Dromasauria and all other Therapsida and in the pelycosaurs there are always two ventral coracoidal elements, and the plesiosaurs are manifestly animals that require a large ventral support for the shoulder girdle. Had they been evolved from any therapsid, they would have retained the two coracoidal elements. The plesiosaur in its evolution must have come from a land ancestor which had already lost one of the coracoidal elements, and, as a large ventral support was necessary with the change of habit, there must first have been developed an antero-ventral process from the scapula such as we find in the chelonian, and later there was a great increase in size of both this process and of the coracoid. The shoulder girdle condition affords to my mind quite conclusive evidence that the plesiosaur was not derived from any therapsid or theromorph.

The pelvis of the plesiosaur, like the shoulder girdle, gives convincing proof that the ancestor was not a therapsid. All primitive therapsids have what is called a plate-like pelvis, where the ventral elements are a large rectangular pubis with a foramen and completely sutured to a somewhat elongated ischium. The early diapsidans also have a similar pelvis. At first sight, the plesiosaurian pelvis looks very similar but, on more careful examination, it is seen to be entirely different. It has a large rectangular pubis and an elongated ischium, but the pubis has no foramen and it is separated from the ischium by an obturator foramen. Though, by convergence, the pelvis has come to resemble that of the primitive Therapsida, it cannot have been derived directly from such a pelvis nor can it have come even from the plate-like pelvis of a primitive diapsidan. It must have come from a triradiate pelvis of a land ancestor,—a pelvis such as is seen in the chelonians and fairly similar to that seen in *Sphenodon*.

The foot structure shows that there has been a large fifth metacarpal and that the land ancestor must have had a foot like *Sphenodon*,—a type of foot never found in any therapsid or theromorph.

CONCLUSIONS ON THE PHYLOGENY AND CLASSIFICATION OF THE REPTILES

All the lines of evidence from the skull, girdles and feet seem to me to point conclusively to the plesiosaur's having been derived from a land ancestor on the diapsidan line, but a little more primitive than the diapsidan, and which had, by a lizard-like habit, independently evolved a triradiate pelvis.

It is further difficult to avoid the conclusion that the chelonian must also have been evolved from just such an ancestor, and, if this be so, we

must regard the plesiosaurs and the chelonians as nearly related groups, though, each having specialized in different ways, they are so very unlike each other.

Eunotosaurus is too imperfectly known to enable us to say anything definite about its affinities. In having eight pairs of enlarged ribs it looks like a primitive chelonian, yet the ribs overlap and were doubtless movable. *Mesosaurus* and a number of other aquatic forms have enlarged ribs, and I do not think the evidence that *Eunotosaurus* is an ancestral chelonian is at all conclusive.

If we now take (1) the Diapsida, as including all the two-arched orders, together with the Squamata, which I believe to be a modification of the same type, (2) the Synapsida, as including the mammal-like Therapsida and the more primitive theromorphs of America, (3) a third group of primitive reptiles with fully-roofed skulls, i.e., the Cotylosauria, and (4) a fourth group which would include the Sauropterygia and the Chelonia, then it will be seen that only a very few forms are left for consideration and, with the exception of the ichthyosaurs, none of them at all fully known.

The Ichthyosauria form a very isolated, highly specialized group of aquatic animals distinctly more primitive than the plesiosaurs. Concerning their origin and affinities we know very little. Years ago, not knowing where else to place them, I gave them a separate origin from the cotylosaurs, as had previously been done by Cope, though I was not then aware of it. The skull has a very manifest upper temporal fossa; the shoulder girdle has lost one of the coracoidal elements, and the pelvis has been derived from a triradiate type. We are probably, therefore, justified in concluding that the ichthyosaur is derived from a lizard-like land form which had advanced some short distance along the diapsidan line, but not quite so far as the point where the chelonians and plesiosaurs were given off.

One or two forms that may perhaps be allied to the ichthyosaurs are *Mesosaurus*, *Protorosaurus*, *Heleosaurus* and *Broomia*. All are primitive long-snouted forms, but in none is the skull fully known. In each the shoulder girdle has only a single ventral element and the pelvis is of the plate-like type. The skull will probably prove to have a single upper temporal fossa.

Having given a little consideration to the more important groups concerning whose affinities there has been some difference of opinion, we may now briefly consider what may have been the main lines of evolution of the reptiles.

The Cotylosauria are held by all to be the most primitive reptilian superorder, or class. They form a rather heterogeneous group, and most of the forms known are too specialized to have been ancestors of any of the later reptilian orders. But there were certainly many small generalized types, and, from one of these, all the later reptiles were derived.

Very early there arose a branch probably of small broad-headed forms which developed a lower temporal fossa for the greater accommodation of the temporal muscle. From these were evolved, first, the thero-morph types so well known from the Lower Permian of America, and later the therapsid types of the Upper Permian and Trias of South Africa. These latter, while retaining the two coracoidal elements and for a long time the plate-like pelvis, became further specialized by having the legs developed for walking and running, with the body well off the ground. From some higher therapsid arose the Mammalia.

From another branch of small lizard-like forms arose all the other reptiles. The early forms had probably a skull essentially like that of *Ichthyosaurus* but without the specializations. *Aræoscelis* of Williston is probably very near to these ancestral forms, and *Mesosaurus* is one of the earliest modifications for aquatic life. *Aræoscelis* still retains the ancestral two coracoidal elements, but very early one of these was lost,—I believe the posterior, as is certainly the case in *Varanops*,—and in all later forms only the one element remains, often much enlarged.

The ichthyosaurs are the result of an extreme aquatic specialization of one of the earlier lizard-like members of the group.

The chelonians and plesiosaurs are specializations from a later lizard-like form,—the one becoming a slow-moving, heavily-armored, swamp-frequenting type, and the other adapted for an aquatic life in comparatively shallow water.

For this group of primitive reptiles a new name seems required. Enaliosauria might be retained in an extended sense, but one can hardly expect the tortoises to be considered as enaliosaurs. In harmony with the terms for the other two large groups of reptiles, the Synapsida and the Diapsida, the name Anomapsida might be given.

The Diapsida, the third large group of the later reptiles, arose in Permian times doubtless from an anomapsid ancestor by the formation of a lower temporal fossa in addition to the upper one. The earlier group seems to have been unsuited for an active land life, and, except the chelonians, which took on a most remarkable specialization, the only other types that were successful were those that became long-headed and adapted for a semiaquatic or aquatic life. But, as soon as the lower

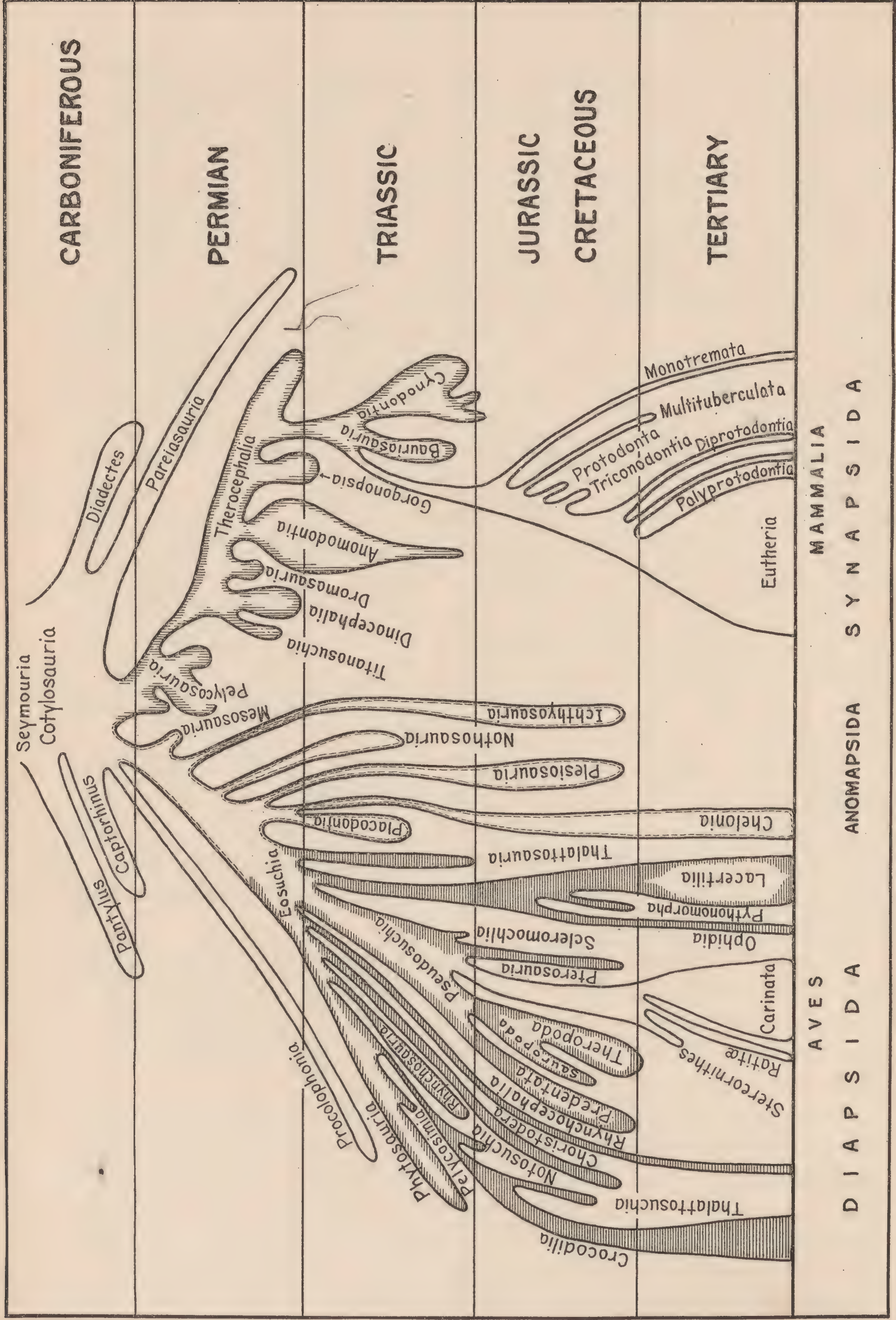


Fig. 13. Evolution and Classification of the Reptilia.

temporal fossa became developed, a large number of varieties of land forms arose, all apparently more or less successful. In fact, so successful did the land forms become that aquatic types became quite exceptional.

The oldest known diapsidan is *Youngina* from the Upper Permian of South Africa. Like the later pseudosuchians it had a long, pointed snout and well-developed running limbs.

Youngina I made the type of an order or suborder, Eosuchia, and from this group arose not only the Pseudosuchia and the primitive crocodiles, the rhynchocephalians and gnathodonts, but also, by the loss of the lower temporal arch and the freeing of the quadrate, the Squamata.

From the pseudosuchians arose the pterodactyls, the dinosaurs and, ultimately, the birds.

In the accompanying diagram, I have indicated what I believe to be the relationships of the principal reptilian orders.

Anyone not very familiar with the subject in reading this paper might readily assume that my views differ very greatly from those of Professor Williston. But this is merely because I have devoted most of my space to the discussion of those few points wherein we disagree and have said practically nothing on the large number of points on which we are in harmony. If the diagram I give be carefully studied and compared with the table given by Williston, it will be seen that, even where we disagree, the disagreement is not so very great. It is merely that he would place a little farther back than I would the origin of the Squamata, the Chelonia and the Ichthyosauria, and that he derives the Plesiosauria from a point near the origin of the Synapsida rather than, as I prefer, from a point some little distance along the line that gave rise to the Diapsida. And, further, on none of the four main points at issue have we any satisfactory paleontological evidence.

Article III.—FURTHER EVIDENCE ON THE STRUCTURE OF THE EOSUCHIA

BY R. BROOM

DEDICATED TO THE MEMORY OF SAMUEL WENDELL WILLISTON

In 1912 I discovered at New Bethesda near Græff Reinet, South Africa, the skull and part of the vertebral column of a small diaptosaurian reptile of the very greatest interest. I gave a short description of the skull in "Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History, II. Permian, Triassic and Jurassic Reptiles of South Africa."¹ Here it is described under the name *Youngina gracilis*. Towards the end of 1914 I exhibited the skull before the Zoological Society of London and there described it at considerable length under the name *Youngina capensis*, forgetting that I had used a different specific name in the American paper. Owing to some delay in the publication of the American Catalogue, the London paper appeared a few weeks before it; so that the fossil must take the name *Youngina capensis*.

The type skull is, on the whole, remarkably well preserved but lacks the upper part and point of the snout and the quadrate region. The mandibles are in position and I did not think it wise to risk injuring the type by exploring the palate, but I believe Prof. D. M. S. Watson, with whom I left the specimen in care, has succeeded in revealing the palatal structure.

The great interest that attaches to this specimen is that it is the only known Permian skull which shows two arches. Other Permian reptiles, such as *Protorosaurus*, *Broomia* or *Heleosaurus*, may have had two arches, but *Youngina* is the oldest reptile in which two arches are clearly shown; and as the large majority of the reptiles known from the Triassic and later periods of the world's history are either reptiles with a two-arched skull or a skull derived from the two-arched type, we have in *Youngina* either an ancestral type or, at least, a type which will throw much light on the structure of the ancestor of the majority of the later reptiles.

As I showed, the skull has two arches not unlike those seen in *Sphenodon*, but *Youngina* differs from the rhynchocephalians in having a

¹1915. Bull. Amer. Mus. Nat. Hist., XXV, pp. 161, 162.

large pineal foramen and in retaining a distinct interparietal bone and tabulars. The squamosal is large and forms most of the posterior border of the lower temporal fossa. The quadratojugal is small. The tabular lies above the squamosal and behind it and articulates with the paroccipital, the parietal and the postorbital as well as with the squamosal, and

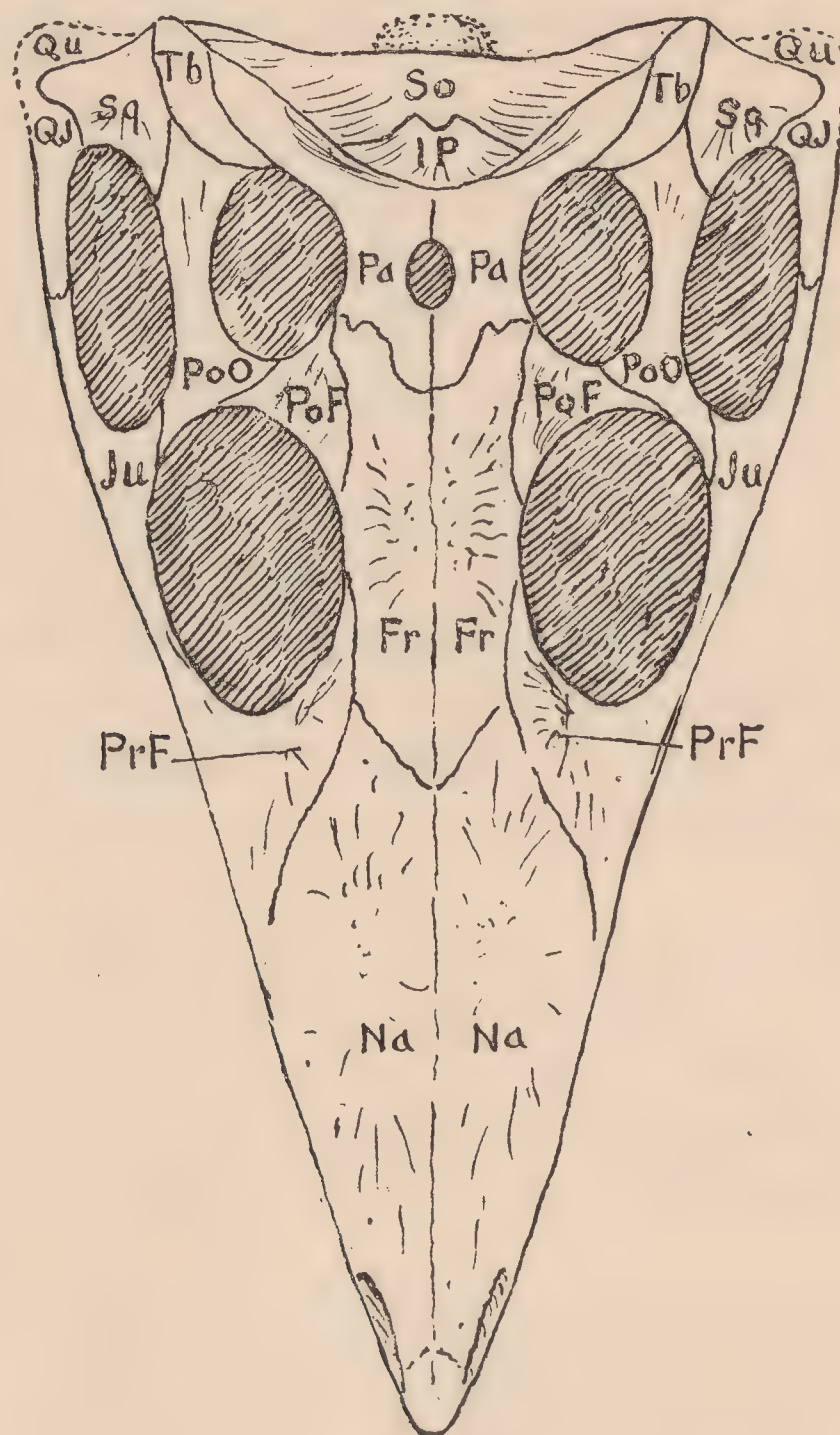


Fig. 1. Skull of *Youngina capensis* Broom. About one and one-half times natural size.

thus reveals to us the origin of such later skulls as are found in *Sauranodon* and *Pleurosauros*, where a large tabular is found above the squamosal, and of the lacertilian skull, where the two bones—a small tabular above and a large squamosal below—are generally retained.

Since the type skull was discovered, two other specimens have been found at the same locality—the second specimen about eight yards from

¹References to lettering in the figure: *Fr.*, Frontal; *Ip.*, Interparietal; *Ju.*, Jugal; *Na.*, Nasal; *Pa.*, Parietal; *Po.F.*, Postfrontal; *Po.O.*, Postorbital; *Pr.F.*, Prefrontal; *Qu.*, Quadrate; *Q.J.*, Quadratojugal; *So.*=*Sa.*, Supra-occipital; *Sq.*, Squamosal; *Tb.*, Tabular.

the type and the third about thirty yards away, but all in the same horizon. The second specimen was apparently a nearly perfect skeleton, but Mr. J. Venter, who discovered it, removed it in a most unskilful manner, with the result that all that remains of it is a few fragments now in the collection of the Pretoria Museum. These fragments, however, are of very great value. Of the skull there remains much of both mandibles, of both maxillæ and premaxillæ and most of the palate. Of the shoulder girdle we have remains of one scapula and much of one coracoid. There are one good humerus and portions of the other, a radius and ulna and some fragments of the fore foot. Two sternal ossifications are preserved in fair condition. Of the pelvis there remain only one fair pubis and a few fragments, but much of both hind limbs is preserved and one tarsus fortunately is preserved in almost perfect condition.

The third specimen which has been found was discovered by myself. It consists of a good skull, which is somewhat crushed and has lost the occipital region with the tabulars and most of the parietals. The specimen is of great value in showing most of the squamosal with some of the quadrate, much of the palatal structure and almost the whole of the snout in good condition.

With the help of these later specimens it is possible to give a much more perfect restoration of the skull than could be done with the type skull alone.

The snout is long and very pointed. The premaxillaries are small and narrow and each has three teeth and possibly four. The nostril is far forward and low down.

The maxilla is long and slender and has about twenty-one round-pointed teeth, which lie in a groove as in *Ichthyosaurus*, but some of the older teeth in front seem to have their bases ankylosed to the bone, like the teeth in *Varanus*.

The structure of the lachrymal and prefrontal cannot be clearly made out. The upper part of the prefrontal is clear enough, but I cannot find any suture dividing it from what one would expect to be the lachrymal. Possibly the lachrymal is already lost, as in *Sphenodon*. More likely, one is present but either small or united with the prefrontal.

There is no trace of a preorbital vacuity.

The nasal bone is unusually large and broad. It is ornamented by a number of radiating ridges and little knobs.

The frontals, parietals, postfrontals and postorbitals have already been described in the type skull, and the one further point which may be

noted is that, like the nasals, they are ornamented by little radiating ridges and bony knobs.

The squamosal, though not quite perfect in this third specimen, luckily has its lower end preserved. The quadratojugal is displaced and crushed and of the quadrate we have little more than the impression of the anterior side. But the additional evidence enables us to restore the articular regions of the skull with considerable confidence.

The palate is not well preserved in either of the new specimens, both showing the bones considerably crushed. Still the main structure is sufficiently revealed. In front are a pair of prevomers not unlike those in *Proterosuchus* but with the internal nares farther back. As in *Proterosuchus*, the prevomers have a row of small teeth. The palatines are very much larger than in *Proterosuchus*, but, when viewed from the under side, they are considerably hidden by the anterior processes of the pterygoids. I cannot find any teeth on the palatines, but these bones are not sufficiently displayed to show for certain that none exists.

The pterygoids are very large and long bones. Posteriorly they appear to agree in structure with those of most primitive diapsidan reptiles. They articulate with the basisphenoid, as in *Sphenodon* and other rhynchocephaloids. There is a strong transverse process which passes almost directly outwards. This process has, as in *Proterosuchus*, a row of fairly large rounded teeth. The anterior part of the pterygoid is, as in *Proterosuchus*, long and broad, and, as in that genus, it has a large number of small rounded teeth which are arranged in rows. A little in front of the articulation with the basisphenoids, the pterygoids approach each other closely in the middle line, and along this inner portion of each bone there are three or four long rows of small teeth. A little farther out, along a thickened portion of the bone, are two or three rows of rather large teeth very similar to the outer rows in *Proterosuchus*, and in addition to these are a few small teeth still farther out.

The ectopterygoid is small and situated well out, as in *Proterosuchus*; and the infraorbital vacuity is also apparently small.

The mandible is not well preserved in either of the specimens I have on hand. The jaw agrees in many respects with that of the crocodile. The splenial is large and extends forward to near the symphysis, but whether it takes part in the symphysis the evidence does not show. There is a large angular not unlike that of *Erythrosuchus*, and there is a lateral vacuity in the jaw.

The vertebræ are not very well seen in the Pretoria specimen, but they are biconcave and apparently notochordal. Large intercentra are present.

The shoulder girdle is not very well preserved. The scapula is represented only by a portion of its cast. It is apparently short and rounded. The coracoid is single and, so far as preserved, resembles that of *Sphenodon*. It has a well-marked foramen.

The left humerus is completely rotated, so that, though the ventral aspect of the animal is displayed, it is the upper or posterior surface that is seen. In general the humerus resembles more closely the lizard type than any other with which I can compare it. Quite manifestly, there have been fairly large cartilaginous pads on each end and it would agree

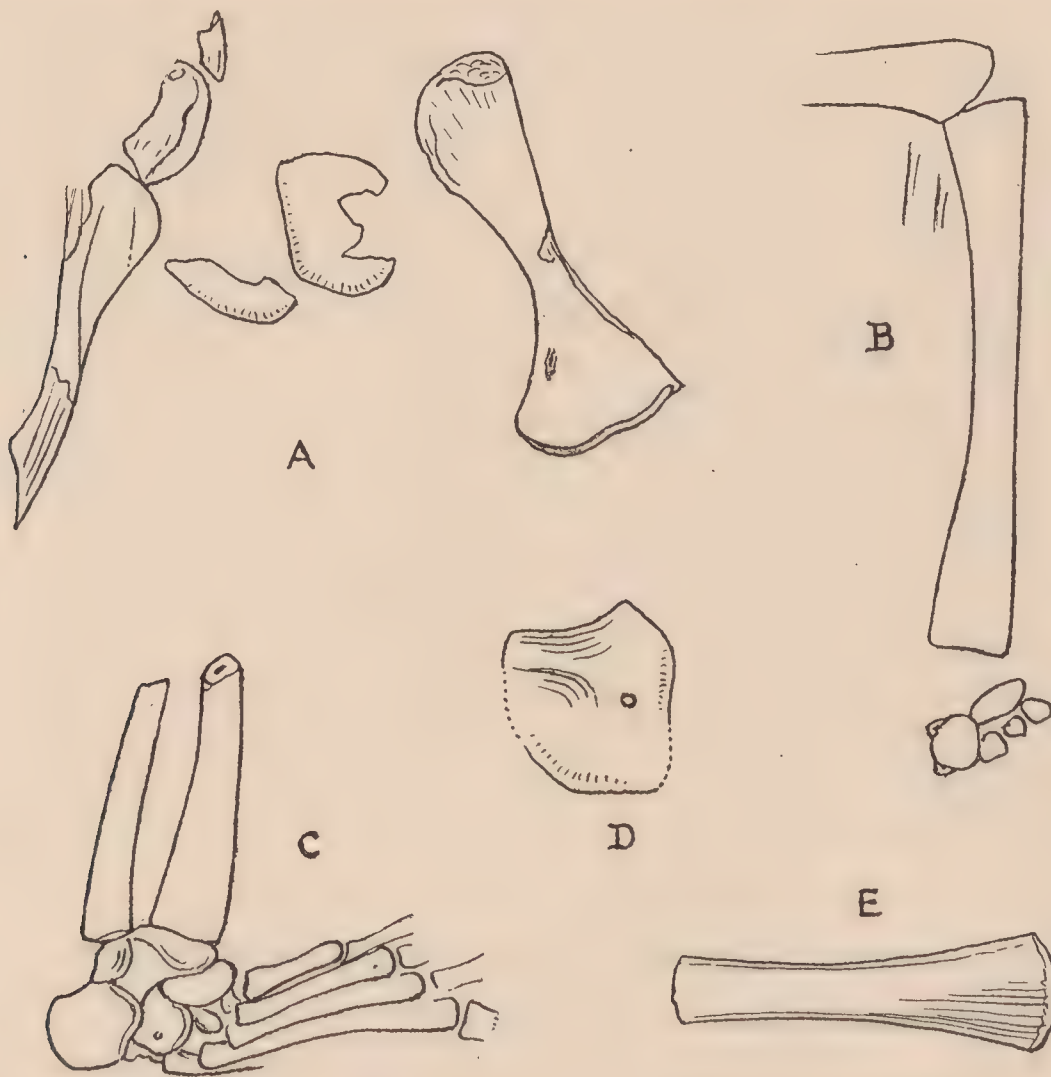


Fig. 2. Figures of portions of the skeleton of *Youngina capensis* Broom. Natural size.

- A. Pectoral region with remains of right coracoid, both humeri and sternal ossifications.
- B. Portions of right limb from front and outer side. The portion of the tarsus is in undisturbed position, the tibiale having fallen out.
- C. The left tarsus and metatarsus with portions of tibia and fibula and of some phalanges, viewed from the inner and plantar surface.
- D. The right pubis.
- E. Distal portion of left femur.

pretty closely with the lizard humerus if the epiphyses were removed. The upper end is expanded somewhat as in *Varanus*, but, as will be seen by the figure, the curving is slightly different. The lower end is much expanded and fairly flat. There is a small ectepicondylar foramen but no entepicondylar. The shaft is much constricted in the middle.

One of the most interesting points in the skeletal structure is the presence of two thin flat ossifications which lie in the sternal region.

These cannot well be anything else than ossifications of the sternum. Neither is perfect, but it is possible to make a restoration from the two which is practically complete. I have figured the remains as they occur. Quite manifestly they are ossifications in cartilage. Though crushed, it is evident they must have been fairly flat and they are thin.

Of the pelvis the only bone that is preserved is the right pubis and this is not quite perfect. The bone is a modification of the plate-like type. It is very slightly broader than long. There are a short but strong anterior and outer process and a very small pubic foramen.

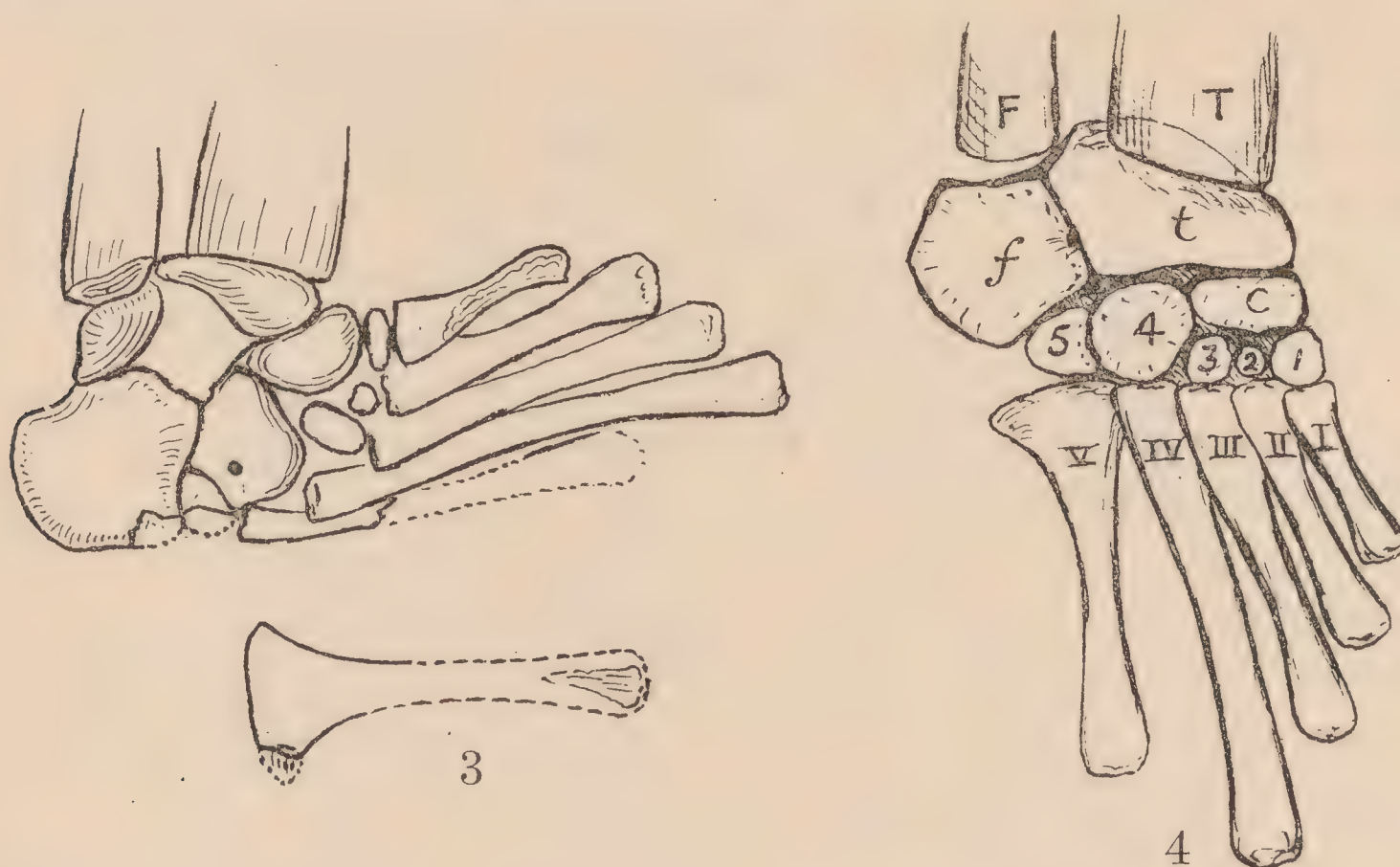


Fig. 3. Left foot of *Youngina capensis* Broom. Slightly more than twice natural size. With, below, fifth metatarsal as viewed from its true under side.

Fig. 4. Tarsus and metatarsus of *Youngina capensis* Broom, as they would appear when viewed from dorsal side. About twice natural size.

The femur, tibia and fibula are all rather slender bones without any striking characters, and they will be best understood by the figures given.

The left tarsus is almost perfectly preserved, with much of the foot, and there is an important portion of the right tarsus also preserved.

Though the left tarsus has its plantar surface exposed, all the elements can be perfectly made out. There are two large proximal elements and five distal tarsals and an eighth large element which occupies the position of the navicular in the human tarsus. The resemblance of the tarsus to that of the Therapsida is so striking that I think we may safely regard the elements as homologous, and I shall therefore speak of the two proximal elements as tibiale and fibulare and the navicular-like element as the centrale.

The tibiale is the largest element of the tarsus. It gives a large articulation to the lower end of the tibia and its outer portion gives part of the articulation for the fibula. The tibiale is curiously twisted, so that, while the plantar surface of the inner two-thirds is nearly in a plane with the plantar surface of the fibulare and the centrale, the plantar surface of the outer one-third is much recessed from the general plane. A foramen passes between the tibiale and the fibulare as indicated in the figures. The tibiale articulates with the fibulare, the large fourth tarsale and the centrale.

The fibulare is a rounded bone whose outer half is thin and flat and whose inner side is thickened to give part of the articulation to the lower end of the fibula and to articulate with the tibiale and the fourth and fifth tarsalia.

The centrale is an element about one-quarter of the size of the tibiale. It articulates with the distal tarsals 1, 2, 3 and 4, and also with the tibiale.

Tibialia 1, 2 and 3 are all small. The appearance as viewed from both above and below is shown in the two specimens.

Tibiale 4 is a large element which articulates with tibialia 3 and 5 and with the centrale, the tibiale and the fibulare. The articulations with all the elements except the fifth tarsal are freely movable, but that with the fifth tarsal must have admitted of very little movement.

The fifth tarsal is a fair-sized element a little larger than either tarsalia 1, 2 or 3. It is firmly united with tarsale 4 by a suture which is straight on the plantar side but curved on the upper. It has a large articulation with the fibulare. Though the outer half is missing, there is probably little doubt that it was a rounded element as figured.

The metatarsals are fairly well preserved. They are moderately straight slender bones which increase in length from the first to the fourth. The fifth is slightly shorter than the fourth. Though not perfectly preserved, enough remains to show that it is a slender bone fairly similar to the other metatarsals but with a larger head. The proximal end is flat and broad and has a short posterior and inferior process which is probably attached by a ligament to the fibulare. In no way is this metatarsal hooked like the fifth metatarsal of *Sphenodon* and most other Diapsida.

The phalanges are long and slender.

When the characters of *Youngina* are looked into, it will be observed that we have in it one of the most important missing links that have yet been discovered. It is undoubtedly a diapsid, and as it is the oldest

diapsid known and the only one yet discovered in Permian beds, it shows, as might be expected, a number of very primitive characters.

The presence of a distinct bone which I believe to be the tabular, above the large squamosal, gives us the clue to the two bones in the lizard skull. Though some doubt may remain as to whether the upper bone is a tabular or a supratemporal, as held by Boulenger and others, no doubt whatever remains that the lower and outer bone is the squamosal. The skulls of *Sphenodon*, of *Pleurosaurus* and of the lizard may be regarded as three different modifications of an ancestral skull of the *Youngina* type.

The shoulder girdle is practically of the same type as is seen in *Sphenodon*. The presence of two large sternal ossifications is very interesting in view of the presence of similar ossifications in some dinosaurs.

The pelvis as shown by the pubis is of the plate-like type found in most Permian forms.

The tarsus is extremely interesting in many ways. In the first place, though undoubtedly a diapsid tarsus, it agrees so closely in structure with the tarsus of therapsids and even of living mammals that the homology of the bones can be determined with certainty, and we are thus able for the first time definitely to fix the homologies of some of the bones in later reptiles.

A few years ago, I figured the tarsus of a small reptile under the name of *Galesphyrus capensis* and referred it to the Dromasauria. But, while it has a general resemblance to the dromasaurian tarsus, all the points in which it differs are points in which it agrees with *Youngina*. There is thus much more probability that *Galesphyrus* is really an eosuchian.

Howes and Swinnerton, when investigating the development of the *Sphenodon* tarsus, found that the large proximal tarsal element in an early embryo is composed of "the intermediare and fibulare chondrified and separated by a foramen . . . the centrale and tibiale being pro-cartilaginous." Their figures, however, do not show a very clear separation of the "centrale" and "tibiale," and anyone who has studied "pro-cartilage" much knows how fallacious the appearances may be. If we assume, as I think is very probable, that the "centrale" and "tibiale" of Howes and Swinnerton are really a single element, then the agreement is fairly close with the tarsus of *Youngina*, but *Youngina* shows that the large supposed intermediare is really the tibiale, and the centrale and tibiale really only the centrale.

Osborn in discussing the tarsus of the primitive "Diaptosauria" says: "No ideally primitive tarsus with three distinct proximal elements (tibiale, intermedium, fibulare), free centrale or centralia, and five separate distal tarsalia, has yet been found among the Diaptosauria. More or less coalescence (astragalus = tibiale + intermedium + centrale) or degeneration of these elements has occurred in every known type. Five separate distal tarsalia are observed only in certain Protorosauria (*Palæohatteria*) and Proganosauria (*Mesosaurus* and *Stereosternum*), a unique feature among reptiles; in all other Diaptosauria distal tarsalia 4 and 5 are united."

Youngina gives us what is probably the most primitive tarsal type where there are still five distal tarsalia, but in addition a distinct centrale. There is no evidence of an intermedium.

The occurrence of a simple unhooked fifth metatarsal in *Youngina* is a point of great importance. The majority of diapsidan reptiles have a peculiarly modified and hooked fifth metatarsal such as is seen in *Sphenodon*. Goodrich considers that the ancestral diapsidan must have had such a character and that all reptiles with this character belong to a common group. As the chelonians also show the character, we must either conclude that they are aberrant descendants of a primitive two-arched reptile or that this modification of the fifth metatarsal has been independently evolved in two different groups. As will be seen from the discussion of this question in my paper on the classification of the reptiles,¹ I favor the latter alternative.

There is good hope that in South Africa we shall yet be able to give a very complete account of the evolution of the Permian ancestors of the diapsid reptiles and perhaps also discover the ancestors of the Ichthyosauria, Plesiosauria and Chelonia.

ADDENDUM

In the three years that have elapsed since the above paper was written, a few additional facts have been discovered which give greater definiteness to certain points in the classification. In the past six months, I have been fortunate in discovering the full details of the structure of the skulls of the tapinocephalian and titanosuchian dinocephalians. These show that the dinocephalians are more nearly related to the anomodonts and to the gorgonopsians and therocephalians than had hitherto been supposed, and not quite so nearly related to the pelycosaurs. The mammal-like reptiles, or Therapsida, have probably

¹1924. Bull. Amer. Mus. Nat. Hist., LI, pp. 39-65.

originated from an at present unknown pro-gorgonopsian or pro-therocephalian group that lived in Lower Permian times. From this primitive group, there arose by three diverging lines of descent: (1) the Dinocephalia, which became subdivided into two suborders, the Tapinocephalia and the Titanosuchia; (2) a line of carnivorous therapsids, branches of which gave rise to the Gorgonopsia, the Therocephalia, the Burnetiamorphia, the Bauriamorpha, the Cynodontia and the Mammalia, and (3) a line which resulted in the specialized group the Anomodontia. The exact relationship of Dromasauria to the other therapsids will remain doubtful until we get the details of the structure of the skull and jaw. (4 Nov., 1923.)

Article IV.—THE POSITION OF THE “SPARASSODONTS”:
WITH NOTES ON THE RELATIONSHIPS AND HISTORY
OF THE MARSUPIALIA

BY HORACE ELMER WOOD, II

Repeated controversies concerning the relationships of the extinct South American carnivorous marsupials (e.g., *Borhyæna*, *Prothylacinus*, *Cladosictis*, *Amphiproviverra*) have arisen during the past thirty years, and no conclusion has yet been reached which satisfies all the students of this problem. The question came up in a discussion between Prof. William K. Gregory and myself and I am writing this paper at his suggestion. He has given invaluable advice and assistance at each stage of the work. I am indebted to Dr. W. D. Matthew for permission to use the fossil “sparassodonts” in the American Museum, as well as for a critical reading of the manuscript. I am also under obligations to Mr. H. C. Raven of the American Museum for various helpful suggestions. The drawings are the work of Mr. Malcolm McGregor Jamieson.

Ameghino (1892) founded a separate suborder of marsupials, the Sparassodonta, composed of the carnivorous South American marsupials. He regarded them as genetically intermediate between typical polyprotodont marsupials and creodonts. He placed the four genera named above in separate families. Sinclair first (1905, 1906) gave convincing evidence that the “sparassodonts” were true polyprotodont marsupials, in no sense ancestral to or allied with the creodonts. He also classified them as members of the family Thylacinidæ, united to *Thylacinus* by many striking resemblances. This had already been suggested vaguely by Lydekker and Bensley. At the time, Matthew (1907) accepted this unreservedly.

Tomes (1906) came to Ameghino’s aid by announcing that the enamel of a single damaged tooth of *Borhyæna* had the histological structure of the fissipedes and the inadapative creodonts, rather than that of the marsupials. This was recently refuted by Carter (1920) from more adequate material. He showed that the enamel structure of *Borhyæna*, *Cladosictis* and *Pharsophorus* was of typical carnivorous polyprotodont type.

Except for Tomes’s paper the reference of the “sparassodonts” to the polyprotodonts passed unchallenged. Their union with *Thylacinus* in the family Thylacinidæ was also accepted until Matthew in “Climate and Evolution” (1915, delivered orally a number of years earlier) denied that the “sparassodonts” were related to any Australian form more

closely than by descent from a common didelphid ancestor. Scott (1913) supported Sinclair's reference of the "sparassodonts" to the Thylacini-dæ. Gidley (1915), Loomis (1921) and Osgood (1922) took a position somewhat intermediate between Sinclair and Matthew, regarding all these forms as "Thylacinidæ," but apparently deriving both Australian and South American forms from hypothetical Paleocene thylacines in Holarctica.

Although Matthew denied the possibility of an *isostatic* connection between Australia and South America on *isostatic* grounds, he admitted the probability of an early Tertiary elevation of the southern continents to the edge of the continental shelf (1915, p. 283); and, although doubting its probability, he considered the possibility of the transportation of a hystricomorph rodent across the Atlantic Ocean from Africa to South America (pp. 229-231). The transportation of a small thylacine from the edge of the continental shelf south of Tasmania to Antarctica, and thence of a descendant across the narrow deep-water channel to South America, is equally conceivable. Although any assumption of this type is difficult to accept and requires strong proof, such a discontinuous bridge would result in a partial mingling of faunas (the particular migrants chosen being determined partly by chance, partly by their adaptability to sea-travel). That something of the kind may have taken place is suggested by the striking resemblance—sometimes extending to specific identity—of the Tertiary invertebrate faunas of Patagonia, New Zealand and Australia,—a similarity not shared with any other region. (For a further discussion of this question see Ortman, 1902, Matthew, 1915, Barbour, 1916, Loomis, 1921.)

I have reviewed the literature on the southern land bridge, but I have not attempted to discuss the subject further, as it involves balancing against one another unproved and contradictory hypotheses. I am not competent to discuss the evidence for or against isostasy, or its implications, or the potency of natural rafts as transporting agents. Any final decision as to relationship should, however, be based chiefly on structure—and the paleontological record, when legible—rather than on present geographic distribution or unproved theories of crustal movement.

Matthew's morphological conclusions, as given in "Climate and Evolution," are as follows:

The near resemblance between the modern Australian *Thylacinus* and the Borhyaenidæ of Tertiary South America has been used as an argument for an Antarctic connection between the two. Such a hypothesis will not bear close examination. The resemblance is not closer than between parallel adaptations in distinct families of true Carnivora whose genealogy has been more or less completely traced back

through independent lines of descent from unspecialized common ancestors. It is not closer, for instance, than that between the Oligocene Felidæ and the modern *Cryptoprocta* of Madagascar, whose common descent from an unspecialized placental carnivore (Viverrid or Miacid), analogous to the marsupial didelphyids, is generally admitted. The common characters distinguishing thylacinids and borhyænids from the didelphyids are, without exception, such as would naturally be assumed independently in adaptation to predaceous terrestrial life and have been so assumed in numerous independent parallel adaptations of the same sort among placental Carnivora. On the other hand, *Thylacinus* has retained certain didelphyid characters which are already lost by the most primitive of the Borhyænidæ (palatal vacuities, posterior position of the orbits, an external lachrymal duct, double perforation of the basisphenoid), while in other features (brain development, cursorial specialization, etc.) it is more progressive. The Borhyænidæ are more progressive in the reduction of the last molar, in the differentiation of enamel from dentine,¹ less so in the cursorial adaptation of the limbs and feet.

Descent from a common ancestral type is undoubtedly shown, but some at least of the above differences point back to Didelphyidæ as this common type. The characters which Sinclair uses to separate the thylacines are the reduced number of incisors, the carnassial specialization of the molars and especially the loss of the metaconid. Every one of these features, besides numerous other common characters which he does not specify, may be paralleled in two or more distinct lines of Carnivora whose common ancestors are not more predaceously specialized than *Didelphys*. The loss of the metaconid occurs in *Cyon*, *Ischyrocyon*, *Simocyon* and *Enhydrocyon* among the Canidæ, in all the post-Oligocene Felidæ, in *Gulo*, *Megalictis*, *Mustela*, etc., among the Mustelidæ, in the later Hyænidæ, in *Hyænodon* and *Pterodon* among the Hyænodontidæ, in *Patriofelis* among the Oxyænidæ, in all the later Mesonychidæ. Each one of these genera is independently descended from genera in which the metaconid is well developed. In every case, it is simply a stage in predaceous adaptation of the molars, nor can it be assigned any other significance in the marsupial carnivores. There is, in short, no evidence for assuming a closer affinity between thylacines and borhyænids than common descent from didelphyid ancestors and there is strong evidence against such an assumption.

Granting that any one, or that several, of the characters linking the "sparassodonts" with *Thylacinus* might be due to parallelism, such an explanation becomes more difficult to accept in geometric ratio as this list is multiplied, unless other characters link the "sparassodonts" with the Didelphidæ while separating them from *Thylacinus*, which is apparently not the case. That the "sparassodonts" lack part of the common didelphid heritage which is retained in *Thylacinus* does not prove them to be an independent and more immediate offshoot from the didelphids, especially since in most of these characters they are more progressive than *Thylacinus*.

In the instances of parallelism given above by Dr. Matthew, the members of each family are still clearly distinguishable as to family, even

¹But see Carter, 1920. H. E. W.

though it may be difficult to state that difference in words. Figs. 1–47—or, better still, the actual specimens,—show that *Thylacinus* fits in most naturally among the “sparassodonts.”

In this paper I have attempted to give a fair summary of the osteological characters of didelphids, “sparassodonts,” *Thylacinus* and dasyurids, usually omitting general polyprotodont characters and those of purely specific or generic value. This is based, for living marsupials and *Amphiproiverra*, on material in the American Museum of Natural History. Most of the characters for *Notoryctes*, *Prokaryon* and *Cladosictis* are taken from Sinclair’s monograph (1906). The numbers, unless otherwise indicated, refer to American Museum specimens. It is often necessary to list separately characters which are, or which may be, complementary to each other.

The following characters indicate thylacine affinities for the “sparassodonts”: 2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 17, 18, 19, 24, 25, 32, 34, 35, 36, 39, 40, 41, 43, 44, 45, 48, 49.

These give no light on this question: 3, 14, 27, 28, 29, 30, 31, 33, 37, 38, 42, 46, 47.

These characters suggest didelphid affinities for the “sparassodonts”: 1, 15, 16, 20, 21, 22, 23, 26.

A valid objection may be raised to this summary as it stands. Where two characters, listed separately, are necessarily complementary to each other, they should be counted as only a single unit. Going over these tables, uniting characters clearly complementary to each other, omitting the neutral characters and italicizing the more important ones, we get the following summary: thylacine affinities: 2, 4, 5, 6, (7 & 8), 9, 10, 11, 12, 13, 17, 18, 19, 24, 25, 32, 34, 35, 36, 39, 40, 41, 43, 44, 45, 48, 49; didelphid affinities: 1, 15, 16, (20 & 21), 22, 23, 26. I omit the neutral characters, as they are either highly variable within the limits of each group, or else the “sparassodonts” differ from all the others (as, for example, in regard to the number of premolars replaced). In this respect the “sparassodonts” are separated as widely from the Didelphidæ as from *Thylacinus*.

Of the characters favoring thylacine affinities these are underlined as more important: the dental formula $I^{\underline{4-3}} C^{\underline{1}} P^{\underline{3}} M^{\underline{4}}$; the reduction of the protocone; the high shearing metastyle; the parastyle plastered on the paracone; the loss of the mesostyle; the approximation of the paracone and metacone; the narrow shearing M^4 ; the absence of the metaconid (see Figs. 1–16); the thickened, but not down-turned, posterior edge of the palate (see Figs. 32–47); the very wide temporal

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NAME AND SPECIMEN	1. LOCALITY	2. DENTAL FORMULA	3. DECIDUOUS TEETH	4. PROTOCONE	5. METASTYLE SHEARING BLADE	6. PARASTYLE	7. Ps:Ms	8. MESOSTYLE	9. PA:ME	10. M ⁴	11. FIRST UPPER INCISORS	12. TIP OF UPPER JAW	13. TRIGONID	14. SYMPHYSIS	15. PALATAL VACUITIES	16. POSTERO-EXTERNAL CORNER OF PALATE	17. POSTERIOR EDGE OF PALATE	18. TEMPORAL FOSSA	19. ANTERIOR TIPS OF NASALS	20. POSTERIOR ENDS OF NASALS	21. NASAL LACHRYMAL BONES	22. POSITION OF ORBITS	23. LACHRYMAL FORAMEN	24. SUPRA-ORBITAL CREST	25. POSTORBITAL PROCESS OF FRONTAL	26. POSTORBITAL PROCESS OF JUGAL
<i>Thylamys keaysi</i> No. 16472	Peru	$I\frac{1}{2}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$		Slightly higher than in <i>Didelphis</i>	Low	Large free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, notched by two foramina	Normal	Protracted	Very slightly spread	Widely separate	Anterior	Double or single; inside orbit	Absent	Absent	Present
<i>Philander</i> species No. 2072	South America	$I\frac{1}{2}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$		Slightly lower than in <i>Didelphis</i>	Low	Fairly large, free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, notched by remnants of two foramina	Normal	Protracted	Very slightly spread	Widely separate	Anterior	Double; just inside orbit	Absent	Absent	Present
<i>Metachirus</i> species No. 244	Colombia	$I\frac{1}{2}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$		As in <i>Didelphis</i>	Low	Large free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, pierced or notched by two foramina	Normal	Protracted	Slightly spread	Widely separate	Median	Double; on edge of orbit	Absent	Small	Absent
<i>Caluromys derbianus</i> No. 10058	Costa Rica	$I\frac{1}{2}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$		Slightly lower than in <i>Didelphis</i>	Low	Small free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Almost lost	Pierced by foramen	High transverse ridge, notched by remnants of two foramina	Normal	Protracted	Widely spread	Distinctly separate	Anterior	Double; on edge of orbit	Slight	Very large	Absent
<i>Chironectes minimus</i> Nos. 30752, 33027	Nicaragua	$I\frac{1}{2}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$		Slightly lower and sharper than in <i>Didelphis</i>	Low	Very large, free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Broad point	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, pierced by two foramina	Normal	Protracted	Widely spread	Almost in contact	Anterior	Single; inside orbit	Absent	Large	Absent or slight
<i>Marmosa chapmani</i> Nos. 4473, 6123	Trinidad	$I\frac{1}{2}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$		As in <i>Didelphis</i>	Low	Large free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, pierced by two foramina	Normal	Protracted	Slightly spread	Widely separate	Median	Double; inside orbit	Slight	Small	Small and blunt
<i>Didelphis virginiana</i> Nos. 238, 240, 616, 7370, 16675 <i>D. mesamericana</i> Nos. 6120, 16743	North America	$I\frac{1}{2}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$	DP3	Prominent, blunt, almost on level with other cusps	Low	Large free cusp	Ps>Ms	Free cusp	Widely separate	Wide Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, pierced by two foramina	Normal	Protracted	Widely spread	Separate or in contact	Anterior	Double; on edge of orbit; or single; inside orbit	Absent	Small or well-developed	Absent or minute
<i>Borhyaena tuberata</i> <i>B. excavata</i> After Sinclair	Patagonia	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$	DC DP3	Minute and very low		Small, plastered on paracone		Absent	Approximated	Shearing	Uniform with other incisors	Rounded	Mtd absent	Fused	Lost	Pierced by foramen	Thickened, no ridge	Very wide	Retracted	Widely spread	Wide or narrow contact	Markedly anterior	?Single; well inside orbit		Absent	Small
<i>Prothylacinus patagonicus</i> After Sinclair	Patagonia	$I\frac{4}{3}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$	DP3	Very low		Fairly large, plastered on paracone		Absent	Approximated	Shearing			Mtd absent	Fused	Lost	Pierced by foramen	Thickened, no ridge	Very wide				Markedly anterior	?Single; well inside orbit			Absent
<i>Cladosictis petersoni</i> <i>C. lustratus</i> After Sinclair	Patagonia	$I\frac{1}{3}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$	DC DP2 DP3	Very low		Fairly large, plastered on paracone		Absent	Approximated	Shearing	Uniform with other incisors	Rounded	Mtd absent	Ligamentous	Lost	Pierced by foramen	Thickened, no ridge	Wide	Retracted	Widely spread	Wide contact	Markedly anterior	?Single; well inside orbit	Large	Fair	Absent or minute
<i>Amphiprovierra mazaniana</i> No. 9254, also after Sinclair	Patagonia	$I\frac{1}{3}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$	DP3	Very low	High	Small, plastered on paracone		Absent	Approximated	Shearing	Approximated	Rounded	Mtd absent	Ligamentous	Lost	Pierced by foramen	Thickened, no ridge	Wide	Retracted	Widely spread	Wide contact	Markedly anterior	Single; well inside orbit	Large	Fair	Minute
<i>Thylacinus cynocephalus</i> Nos. 35504, 42259	Tasmania	$I\frac{1}{3}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$	DP3	Very low	High	Fairly large, plastered on paracone		Absent	Approximated	Shearing	Uniform with other incisors	Rounded	Mtd absent	Ligamentous	Present	Bar enclosing foramen nearly lost	Thickened, no ridge	Wide	Retracted	Slightly spread	Widely separate	Median	Double; one inside orbit, one outside	Present	Fair	Sharp spike
<i>Dasyurus viverrinus</i> Nos. 16669, 35721, 42998	Australia	$I\frac{1}{3}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$	DP3	Much lower than in <i>Didelphis</i> , with accessory pl, ml	High	Forms transverse ridge with paracone	Ps<Ms	Free cusp	Separate	Shearing	Uniform with other incisors	Rounded	Mtd>Pad	Ligamentous	Present or closed and spongy	Pierced by foramen; bar sometimes lost	Low transverse ridge, notched by two foramina	Fairly wide	Retracted	Slightly spread	Widely separate	Slightly anterior	Single; inside or on edge, or outside	Present	Fair	Sharp spike
<i>Sarcophilus ursinus</i> Nos. 35106, 35535	Tasmania	$I\frac{1}{3}C\frac{1}{1}P\frac{3}{2}M\frac{1}{1}$	None	Very low and small	High	Forms transverse ridge with paracone		Absent	Approximated	Shearing	Uniform with other incisors	Rounded	Mtd minute	Fused	Present	Bar enclosing foramen nearly lost	Low transverse ridge, notched by two foramina	Very wide	Retracted	Slightly spread	Widely separate	Slightly anterior	Single; on edge of orbit	Present	Good	Sharp spike
<i>Phascogale cristicaudata</i> No. 15009 <i>P. ? macdonnellensis</i> No. 15011 <i>P. flavipes</i> <i>P. swainsoni</i> Raven Collection	Australia	$I\frac{1}{3}C\frac{1}{1}P\frac{3}{3}=2M\frac{1}{1}$		Much lower and sharper than in <i>Didelphis</i>	High	Forms transverse ridge with paracone	Ps<Ms	Free cusp	Separate	Shearing	Approximated	Rounded	Mtd>Pad	Ligamentous	Present	Pierced by foramen; bar sometimes lost	Low transverse ridge, unnotched	Fairly wide	Retracted	Widely spread	Widely separate	Markedly anterior	Double; inside orbit	Present	Absent	Small, blunt
<i>Antechinomys laniger</i> No. 15012	Australia	$I\frac{1}{3}C\frac{1}{1}^{(P-form)}P\frac{3}{3}M\frac{1}{1}^{(P-form)}$		Much lower than in <i>Didelphis</i>	Fairly high	Forms transverse ridge with paracone	Ps<Ms	Free cusp	Separate	Shearing	Approximated	Pointed	Mtd>Pad	Ligamentous	Closed by thin sheet of bone	Bar enclosing foramen lost	Low transverse ridge, unnotched	Fairly wide	Retracted	Very slightly spread	Widely separate	Anterior	Double; one inside, one outside orbit	Present	Absent	Wide, low
<i>Sminthopsis crassicaudata</i> No. 15013	Australia	$I\frac{1}{3}C\frac{1}{1}P\frac{3}{3}M\frac{1}{1}$		Distinctly lower and sharper than in <i>Didelphis</i>	Fairly high	Forms transverse ridge with paracone	Ps<Ms	Free cusp	Separate	Shearing	Approximated	Pointed	Mtd>Pad	Ligamentous	Present	Bar enclosing foramen lost	Low transverse ridge, notched by two foramina	Fairly wide	Retracted	Very slightly spread	Widely separate	Anterior	Single; on edge of orbit	Present	Absent	

NAME AND SPECIMEN	27. POSTORBITAL CONSTRICTION OF SKULL	28. TYMPANIC BULLA AND COMPONENTS	29. PAROCCIPITAL PROCESS	30. CONDYLAR FORAMEN	31. OCCIPUT	32. ATLAS	33. BACKWARDLY DIRECTED SPIKE ON ATLAS INTER- CENTRUM	34. ATLANTAL TRANSVERSE PROCESS	35. NEURAL PROCESS OF AXIS	36. NEURAL PROCESSES ON C3-7	37. LONGEST NEURAL PROCESS ON	38. VERTEBRAL ARTERY PIERCING TRANSVERSE PROCESS OF	39. VERTEBRAL FORMULA	40. ANTECLINAL VERTEBRA	41. SACRAL VERTEBRÆ COSSIFIED WITH PELVIS	42. ACROMION	43. ILLIUM IN CROSS-SECTION	44. ACETABULUM	45. MARSUPIAL BONES	46. PATELLA	47. ECTOCUNEIFORM	48. HALLUX	49. TERMINAL PHALANGES
<i>Thylamys keaysi</i> No. 16472	Slight	Well-developed; alisphenoid, tympanic, periotic, mastoid																					
<i>Philander</i> species No. 2072	Slight	Perfect; alisphenoid, tym- panic, periotic	Absent			Solid ring	Absent	Short and little con- stricted proximally	Reduced to small ridge.	Almost lost	C7	C2-7	D12, L7, S2	D11?	2		Flattened tri- angle	Widely open on to ischium	Large	Unossified		Complete, divergent	
<i>Metachirus</i> species No. 244	Some	Incomplete alisphenoid bulla as in <i>Didelphis</i>	Long, rod-like, directed down and back	Double	Descends to level of basis cranii																		
<i>Caluromys derbianus</i> No. 10058	Some	Incomplete alisphenoid bulla, slightly better than in <i>Didelphis</i>	Long, longitudi- nally plate-like, directed back and down	Double	Descends to level of basis cranii																		
<i>Chironectes minimus</i> Nos. 30752, 33027	Very great	Incomplete alisphenoid bulla, slightly better than in <i>Didelphis</i>	Short, rod-like, directed down	Double	Does not descend to level of basis cranii																		
<i>Marmosa chapmani</i> Nos. 4473, 6123	Some	Incomplete; alisphenoid, tympanic	Short, longitudi- nally plate-like, directed down	Double	Does not descend to level of basis cranii	Solid ring	Absent	Short and little con- stricted proximally	Hooked back over C3	Reduced and stubby	C2	C2-7	D12, L7	D11?		Fairly short, wide, tri- angular	Flattened tri- angle	Open on to ischium	Large	Unossified			
<i>Didelphis virginiana</i> Nos. 238, 240, 616, 7370, 16675 <i>D. mesamericana</i> Nos. 6120, 16743	Considerable	Incomplete alisphenoid bulla	Long, rod-like, par- occipital directed down and slightly back	Double	Descends to level of basis cranii	Solid ring	Minute or absent	Short and little con- stricted proximally	Stout, not projecting back over C3	High and thick	C3, 4	C2-7	D12, L7, S2	D11	2	Short, wide, triangular	Flattened tri- angle	Open on to ischium	Large	Unossified	Variable; unsupport- ed by cuboid (3 specimens) or largely supported (1 spec- imen)	Complete, divergent	Uncleft
<i>Borhyaena tuberculata</i> <i>B. excavata</i> After Sinclair	Some	Alisphenoid bulla com- menced	Transverse, plate- like, well-devel- oped	Double	Descends far be- low basis cranii, even below con- dyles	Free inter- centrum	Present	Long and constricted proximally	Halberd-shaped, hooked back over C3	Long and spiked	C7	C2-7											Cleft
<i>Prothylacinus pata- gonicus</i> After Sinclair			Short, stout, rod- like, directed back, down, and out	Double	Descends below level of basis cranii	Solid ring	Absent	Long and constricted proximally	Halberd-shaped, hooked back over C3	Long and spiked		C2-7		D10	1		Flat	Open on to obtur- ator foramen		Ossified	Partly supported by cuboid	Reduced to metatarsal	Cleft
<i>Cladostictis petersoni</i> <i>C. lustratus</i> After Sinclair	Considerable					Solid ring	Absent	Long and constricted proximally	Halberd-shaped, hooked back over C3	Long and spiked	C7	C2-7	D13, L6, S2	D10	1	Long, narrow parallelogram	Flat	Open on to obtur- ator foramen	Absent		Partly supported by cuboid	Reduced to metatarsal	Uncleft
<i>Amphiproteron mazatlanense</i> No. 9254, also after Sinclair	Great	Alisphenoid bulla com- menced	Transverse, plate- like, well-devel- oped	Single	Descends far be- low level of basis cranii, even below con- dyles	Free inter- centrum	Absent	Long and constricted proximally												Ossified	Chiefly supported by cuboid	Divergent, dis- tal end un- known	Uncleft
<i>Thylacinus cynoceph- alus</i> Nos. 35504, 42259	Some	Alisphenoid bulla not quite complete	Long, diagonal, rod-like, with ex- panded base, di- rected down and back	Double	Descends to level of basis cranii	Free inter- centrum	Present	Long and constricted proximally	Halberd-shaped, hooked back over C3	Long and spiked	C7	C2-7	D13, L6, S2	D10	1	Short, stout parallelogram	Flat	Open on to obtur- ator foramen	Vestigial	Unossified	Chiefly supported by cuboid	Absent	Cleft
<i>Dasyurus viverrinus</i> Nos. 16669, 35721, 42998	Considerable	Perfect alisphenoid-tympanic bulla	Diagonal, rod-like, with expanded base, directed down and back	Double	Descends far be- low level of basis cranii	Solid ring	Large or absent	Long and constricted proximally	Halberd-shaped, bent back over C3	Long and spiked	C7	C2-6 C7 pierced or not	D12, L7, S2	D9	1	Long, narrow, triangular	Rather flat	Open on to obtur- ator foramen	Large	Unossified	Partly or slightly sup- ported by cuboid	Reduced to metatarsal	Cleft
<i>Sarcophilus ursinus</i> Nos. 35106, 35535	Very great	Perfect alisphenoid-tympanic bulla	Stout, short, rod- like, directed back and down	Double	Descends below level of basis cranii	Solid ring	Present	Long and constricted proximally	Halberd-shaped, bent back over C3	Spiked	C7	C2-7 Bar below lost on C7	D11, L8, S3	D9	2		Rather flat	Open on to obtur- ator foramen	Large	Unossified	Partly supported by cuboid	Reduced to metatarsal	Cleft
<i>Phascogale cristicav- data</i> No. 15009 <i>P. ? macdonnellensis</i> No. 15011 <i>P. flavipes</i> <i>P. swainsoni</i> Raven Collection	Some	Perfect: alisphenoid, tym- panic, periotic, squamosal, exoccipital, mastoid	Absent, region in- volved in bulla	Double	Crowded high up skull by bulla	Solid ring	Short	Medium and con- stricted proximally	Halberd-shaped, somewhat or not at all bent back over C3	Lost except on C7	C2	C2-6	D12, L7, S2	D9?	1	Long, narrow, triangular	Rather flat	Open on to obtur- ator foramen		Unossified	Partly or slightly sup- ported by cuboid	Complete but small, not divergent	
<i>Antechinomys laniger</i> No. 15012	Some	Perfect: alisphenoid, tym- panic, periotic, squamosal, exoccipital, mastoid	Absent, region in- volved in bulla	Double	Crowded high up skull by bulla				Almost lost	Almost lost	C2		D13, L6	D9			Rather flat	Open on to obtur- ator foramen		Unossified		Absent	
<i>Sminthopsis crassi- caudata</i> No. 15013	Some	Perfect: alisphenoid, tym- panic, periotic, mastoid	Absent, region in- volved in bulla	Double	Crowded high up skull by bulla					Absent			D13, L6, S3			Long, narrow, triangular	Rather flat	Open on to obtur- ator foramen		Unossified		Complete but very small, not divergent	

fossæ; the retracted tips of the nasals (see Figs. 17–31); the free atlanteal intercentrum of *Borhyæna*, *Amphiproviverra* and *Thylacinus*; the long, proximally constricted, transverse process of the atlas; the halberd-shaped neural process of the axis; the long spiked neural processes of the cervical vertebræ 3–7; the number of rib-bearing vertebræ; the flat ilium; the position of the acetabular notch, and the great reduction of the marsupial bones. These characters may be considered as defining the family Thylacinidæ. In all these, the Thylacinidæ (of Sinclair) differ from all the didelphids examined (whatever their habits and food) and very often from *Dasyurus* and even from *Sarcophilus*, which are just as purely carnivorous as any of the Thylacinidæ and should, therefore, possess all the "habitus" characters which are an essential part of the equipment of a carnivorous polyprotodont marsupial. Most of these characters are apparently not immediately dependent on one another; and although, unquestionably, many of them are associated with the carnivorous habits of the Thylacinidæ, they are not *all*, at least, *necessary* modifications for a carnivorous life in a polyprotodont marsupial, since, of these nineteen characters, eight differ from both *Dasyurus* and *Sarcophilus*. These are: the dental formula; the parastyle plastered on the paracone; the absence of the mesostyle; the absence of the metaconid; the thickened, but not down-turned, posterior border of the palate; the number of rib-bearing vertebræ; the flat ilium, and the great reduction of the marsupial bones. Only *Sarcophilus*, of the dasyurids examined, has the abnormally wide temporal fossæ of the thylacinids; and none of the dasyurids has the free atlanteal intercentrum found in *Borhyæna*, *Amphiproviverra* and *Thylacinus* (but fused in *Prothylacinus* and *Cladosictis*).

I found only seven characters tending to support Matthew's view of the didelphid affinities of the "sparassodonts." These are: the geographical separation of Australia and South America; the closed palate of the "sparassodonts" (approximated in *Caluromys*, *Antechinomys* and some specimens of *Dasyurus*); the virtual loss of the bar enclosing the foramen at the postero-external corner of the palate in *Thylacinus*; the naso-lachrymal contact seen in the "sparassodonts" and a few didelphids; the position of the orbits; the arrangement of the lachrymal foramina; and the shape of the postorbital process of the jugal. The geographical occurrence of the forms under discussion is not a morphological character, and its possible meanings are discussed elsewhere. The closed palate is presumably secondary and independently acquired in each family (in the "sparassodonts," *Dasyurus* and *Caluro-*

mys). In any case, it separates the "sparassodonts" from the didelphids nearly as completely as from *Thylacinus*. The loss of the bar from the palate is valid as far as it goes, but such losses occur rather easily. The relative position of the orbits is largely determined by the lengthening or shortening of the face, which are decidedly "habitus" characters. It is, therefore, rather variable and not a very safe guide. The nasolachrymal contact is a valid character, although its value is somewhat reduced by its great variability, not only within the family but inside the genus, species, and even between the two sides of the same individual. The same thing is true of the position of the lachrymal foramina and the shape of the postorbital process of the jugal.

Without denying some weight to the arguments given above for the Didelphidæ as the nearest relatives of the "sparassodonts," I feel that this summary shows a strong preponderance of characters uniting them to *Thylacinus*. The reader must decide whether parallelism will explain so striking a similarity.

Scott (1917), apropos of Nuttall's blood tests, says: "A close relationship is shown to exist between all Marsupials, with the exception of the Thylacine." This would seem to furnish support for the view that *Thylacinus* is not a dasyurid and hence is probably a "sparassodont." Its value as evidence is greatly diminished, however, by the fact that, except for didelphids, *Thylacinus* and *Parameles* were the only polyprotodonts tested, and that the serum was considered of unsatisfactory quality by Nuttall (1904).

The Cænolestidæ of South America are also of interest in this connection. They furnish a parallel case, either connecting with the Australian Peramelidæ and Phalangeridæ, or being parallel derivatives from some opossum. Osgood (1921) and Gregory (1922) both see their closest relatives among the Australian forms. This strengthens, by just so much, the argument for some real relation between the two faunas.

Osgood (1921) emphasizes what he regards as the isolated position of *Myrmecobius*, not only from the dasyurids, but from the marsupials in general, going back to a Jurassic ancestor with more than seven cheek teeth. The reasons for regarding *Myrmecobius* as an aberrant dasyure have been given by Bensley (1903), Gidley (1915) and Gregory (1920). Osgood's monograph does not seem to invalidate their reasoning. He admits that *Myrmecobius* is derived from generalized marsupials, yet one of the most uniform and, presumptively, most primitive marsupial characters is the presence of not more than seven post-canine teeth. Consider also these statements on page 131 of his article: "Whatever the

case may have been with respect to the history of the extra molar teeth of *Myrmecobius*, the view that all the living families of Marsupials were well differentiated early in the Tertiary seems to be well founded. Therefore, without reference to possibly archaic characters other than the teeth, it is still possible to believe in an early predidelphid origin for *Myrmecobius*." Since opossums are known from the Upper Cretaceous, this does not bar them from ancestry to all other marsupials. It may be justifiable, in view of the possible geological antiquity of the type (*Myrmecoboides*, Gidley, 1915), and the unusual "habitus" characters, to make a separate family, the Myrmecobidæ, as has already been done for the Thylacinidæ; although it would be equally logical to regard it as a subfamily of the Dasyuridæ.

In this connection, I wish to point out that more time can be allowed for the radiation of the marsupials than has often been assumed. We know that the opossum, at least, has come down from the Upper Cretaceous without material change. *Wynyardia* is firmly imbedded in the literature as an Eocene or Oligocene diprotodont with polyprotodont affinities and has often been used as a means of dating the origin of the diprotodonts. A discussion of Spencer's paper (1900) between Dr. William K. Gregory and myself led to an attempt to discover these supposed polyprotodont affinities. Spencer lists the following "dasyurid" characters in *Wynyardia* (see Figs. 48-57):

"1. Proportionate length to the breadth of the skull 100:67. This approximates most nearly to *Dasyurus* and shows a decidedly greater proportionate width than in the Phalangeridæ." There is a much closer resemblance both in ratio and proportions to such a diprotodont as *Bettongia* (No. 6346), or *Phascolarctus cinereus* (No. 42178). Even if this were not true, however, such a ratio would mean nothing, since *Dasyurus* and *Wynyardia* have entirely different shapes as seen from above. An accidental equivalence of ratios of length to breadth, if it occurred, would mean nothing. A superficial approach to this ratio is found in *Phascogale*, *Thylacinus* and *Borhyæna*. It is presumably secondary in all these forms. In *Phascogale* it is associated with the enormous bullæ—a "habitus" feature.

"2. Lambdoidal crest well developed, as in *Dasyurus*." It is equally so in *Trichosurus vulpecula*, No. 249, and *Pseudochirus cooki*. This, therefore, is hardly valid as a dasyure character.

"3. Sagittal crest strongly developed, resembling that of Dasyuridæ and species of *Didelphys*." On the whole, it is probably more like *Trichosurus*, since the sunken area in the frontal region between

the V-shaped forks of the sagittal crest is much alike in *Trichosurus* and *Wynyardia*.

"5. The wide sweep and upward curvature of the zygomatic arches, as in Dasyuridæ." This is the only one of these characters that appears to be valid. Even here, however, *Wynyardia* is probably closer to *Bettongia*, or even *Trichosurus*.

"7. The transverse elongation of the glenoid cavity, the downward-produced plate of bone which forms the boundary, is not connected with any structure forming part of the auditory passage. In this respect, it agrees with Dasyuridæ and *Perameles*, and differs markedly from the Phalangeridæ, amongst which it forms the anterior part of a bony auditory canal." By this the author apparently means that in *Wynyardia* and the Dasyuridæ the tympanic ring is not coössified with the postglenoid process as it is in *Trichosurus*. As they are not coössified in *Phascolarctus cinereus*, No. 42178, and various other diprotodonts, the value of this character as a link with the polyprotodonts is nullified.

Among the more striking diprotodont characters are: the chunky premaxillæ; the masseteric process beneath the zygoma; the profile of the skull from above; the V-shaped basin in the frontal region inside the forking sagittal crest; the naso-lachrymal contact (probably secondary for marsupials and primitive for diprotodonts); the descending curve of the sagittal crest to the rear, as seen from the side, and the entirely diprotodont shape of the mandible. Compare the figures of *Dasyurus*, *Wynyardia* and *Trichosurus*.

Wynyardia is also much more recent than the date—Eocene or Oligocene—ascribed to it by Spencer. Frederick Chapman, the Australian geologist, in an oral communication to William K. Gregory, refers it to the *Turritella warburtoni* zone of the Lower Pliocene. This geological level, entirely aside from the morphological evidence cited above, eliminates *Wynyardia* as a possible link between polyprotodonts and diprotodonts. It seems reasonable to regard it as a slightly primitive phalanger.

There is therefore no reason why the preliminary stages in the adaptive radiation of the marsupials may not have taken place by the Upper Cretaceous or Paleocene, except that the scanty marsupial remains of that time are apparently all didelphids (except *Myrmecoboides*, if it is a marsupial). This hypothesis is an expansion of the suggestion of Gidley (1915) and Loomis (1921) that a marsupial adaptive radiation from didelphids into dasyures, thylacines and pre-diprotodonts may

have taken place in the northern hemisphere, after which the didelphids, thylacines and pre-diprotodonts would have entered South America, while the dasyures, thylacines and pre-diprotodonts would have entered Australia. This hypothesis combines the strongest elements in the views of Sinclair and Matthew, avoiding their more difficult assumptions, but a new difficulty, in view of the rather frequent occurrence of the Didelphidæ, is the absence from the northern hemisphere of the remains of the other three families postulated. To fall back on "the imperfection of the geological record" in a way merely begs the question. Possibly these unknown and hypothetical forms may have belonged to the long-lost upland fauna of the later Cretaceous.

The alternative to the hypothesis tentatively expressed above is some more direct connection between the faunas of Australia and South America.

CONCLUSIONS

1. The closest structural relations of the "sparassodonts" are with *Thylacinus*, and, in the absence of any direct evidence of "parallelism," they should be included with it in the family Thylacinidæ, defined as above. *Thylacinus*, however, was not descended from any known "sparassodont."

2. *Myrmecobius* is closely related to the Dasyuridæ in its "heritage" features. It is not a "Mesozoic survival,"—certainly not in the sense that its extra teeth are inherited directly from a Jurassic form with extra teeth.

3. *Wynyardia* is now assigned to the Pliocene instead of the Eocene or Oligocene. It is a true diprotodont in every way, and does not connect the diprotodonts and polyprotodonts.

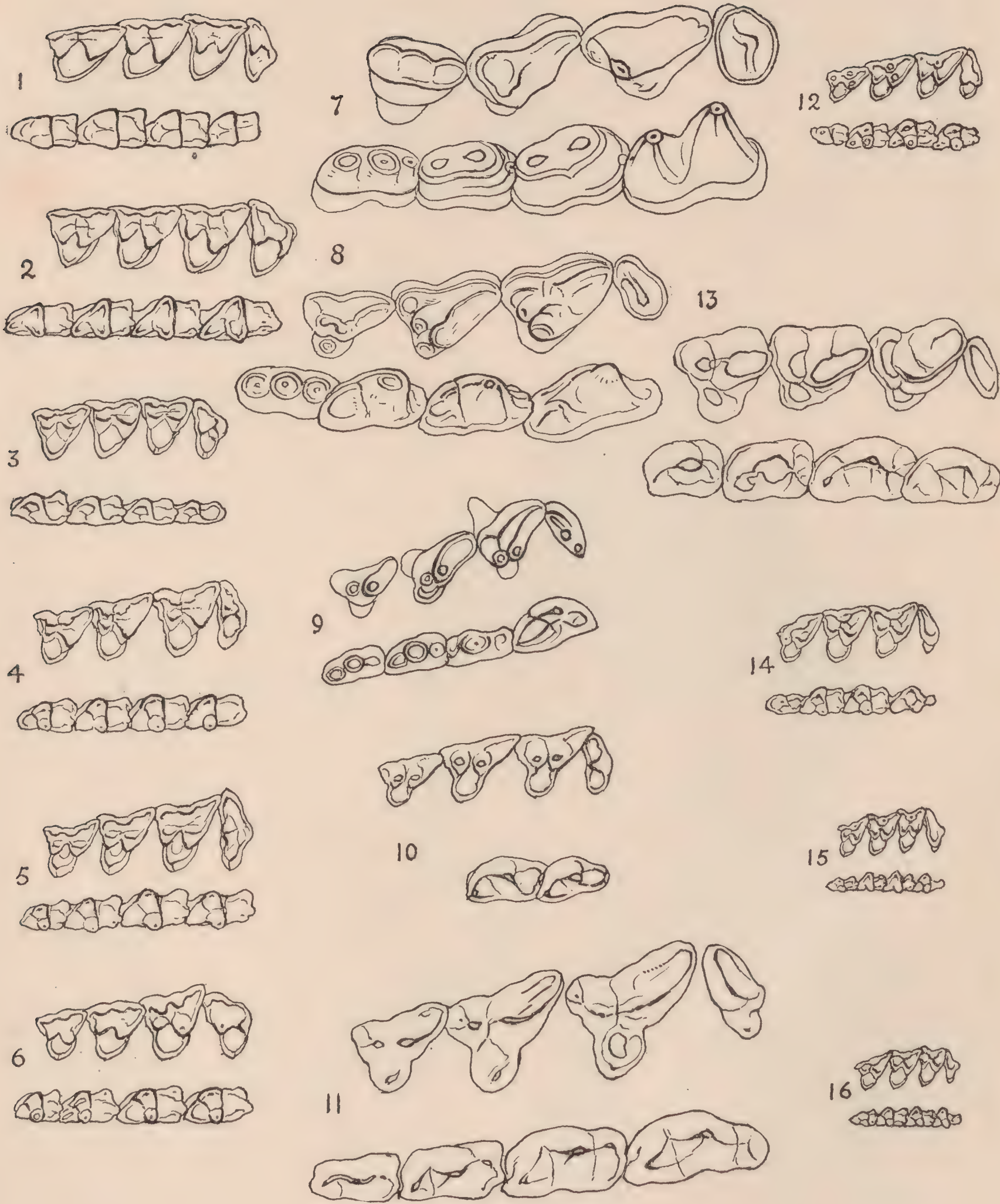
4. The paleogeographic concomitants of the statements above are uncertain. There may have been a discontinuous southern connection between South America and Australia during the late Cretaceous or early Tertiary. Or perhaps the marsupial adaptive radiation began in Holarctica by the Upper Cretaceous. By the Paleocene the Didelphidæ and, perhaps, the Dasyuridæ, Myrmecobidæ, Thylacinidæ and the pre-diprotodonts were already in existence. The competition of the placentals would then have limited the marsupials (except the opossum) to South America (with opossums, thylacines and pre-diprotodonts) and Australia (with myrmecobids, dasyures, thylacines and pre-diprotodonts).

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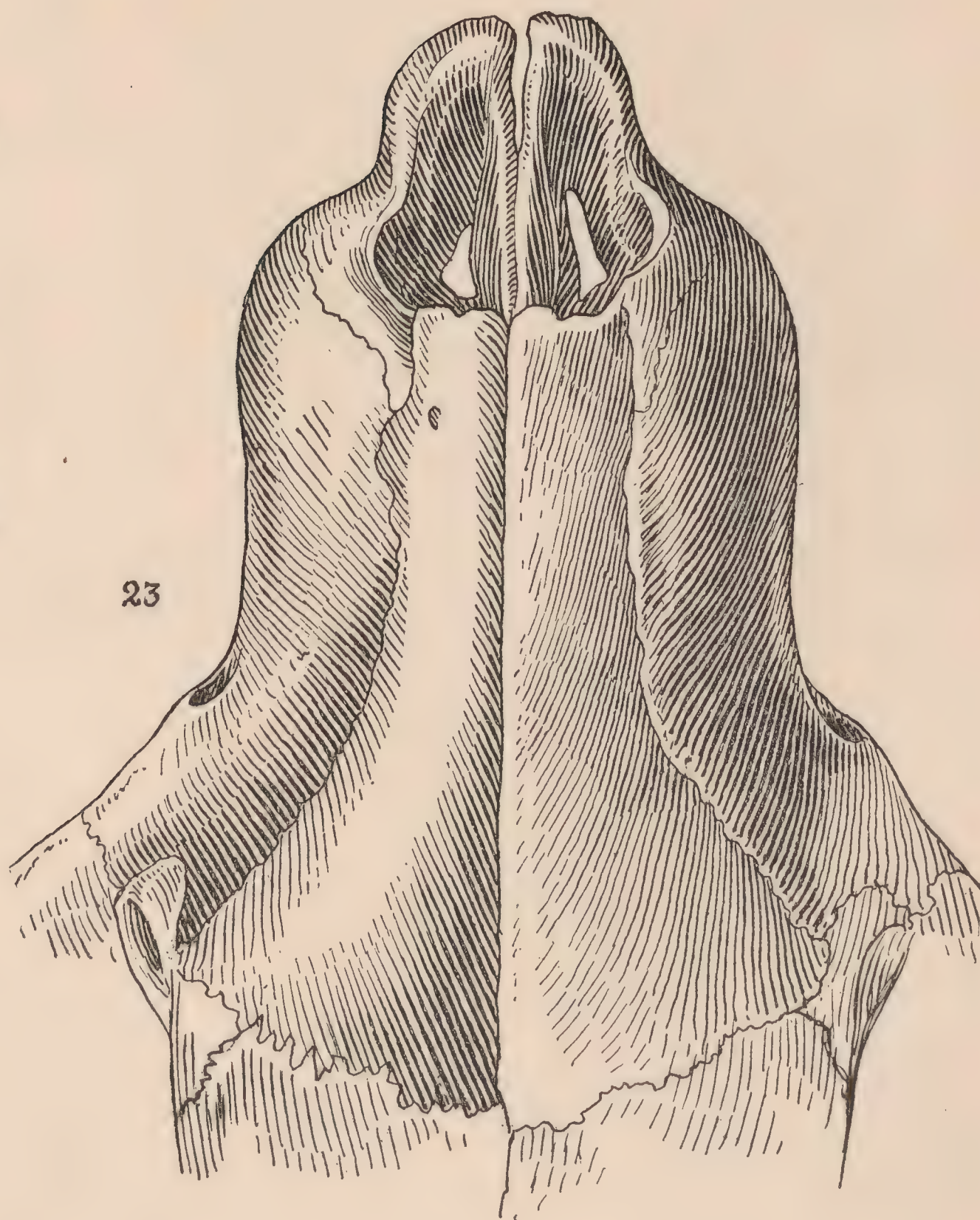
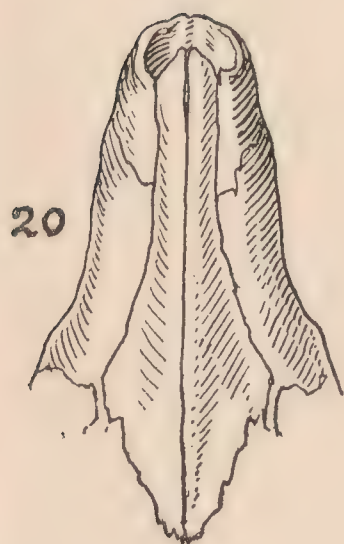
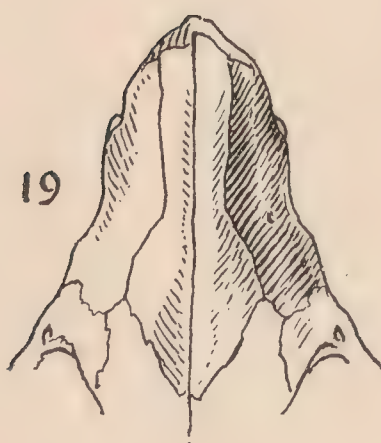
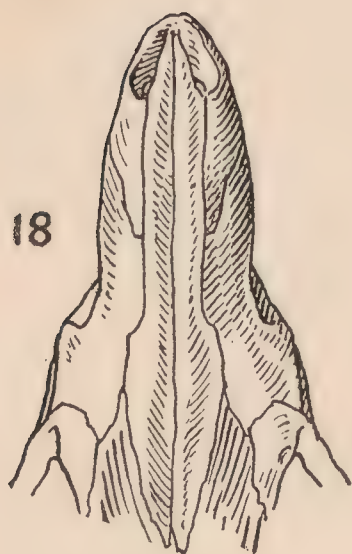
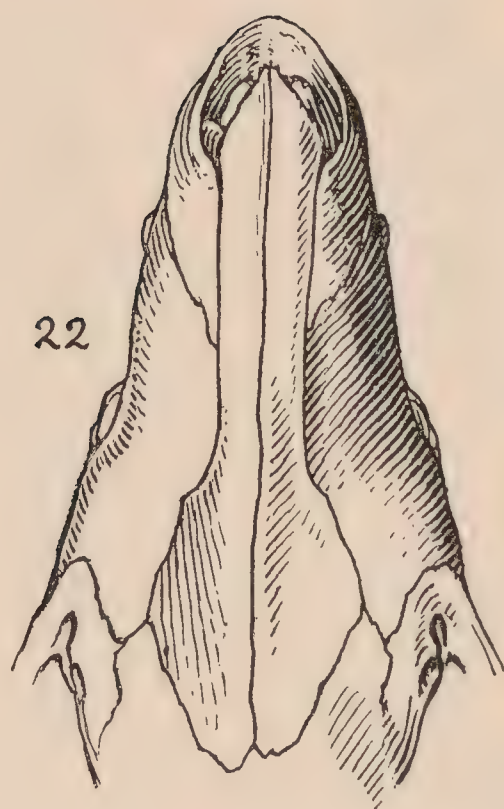
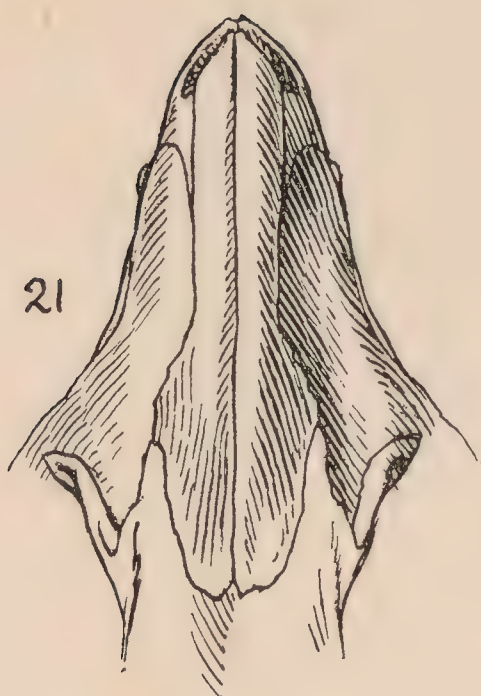
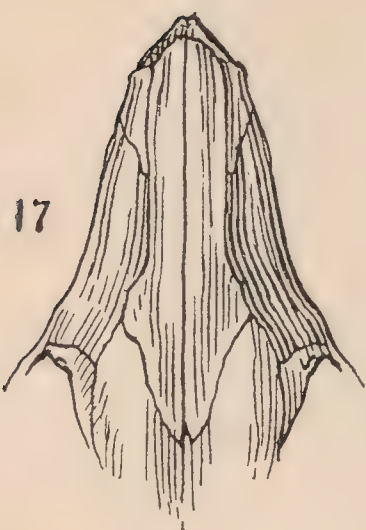
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FIGURES 1 TO 57

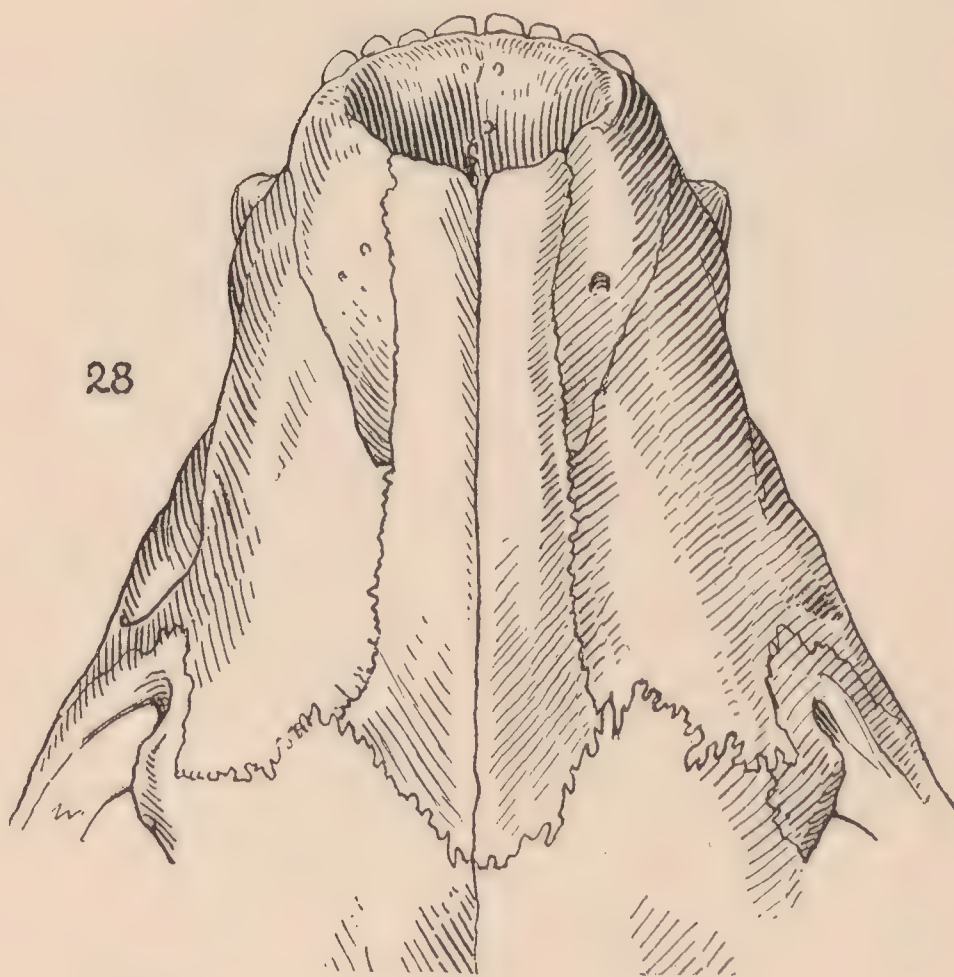
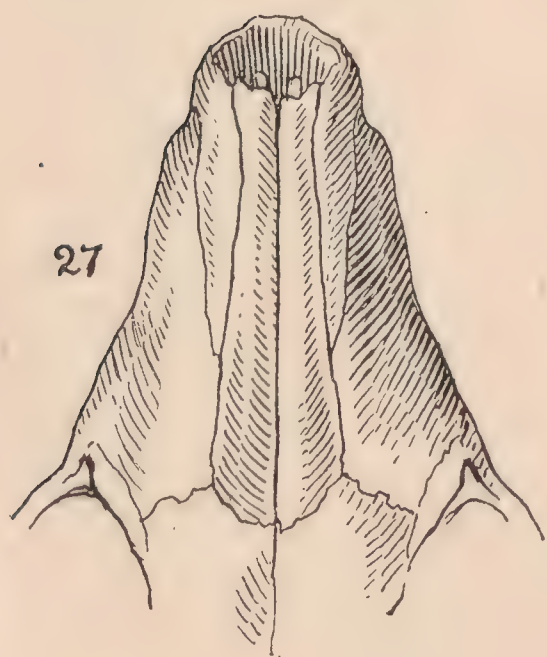
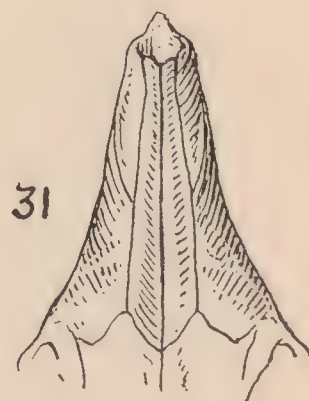
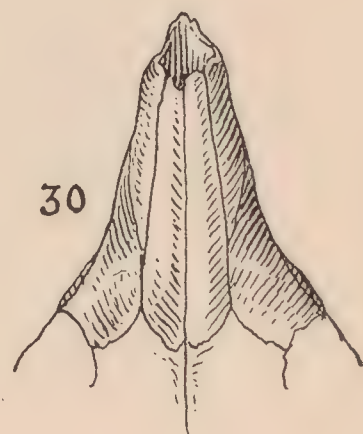
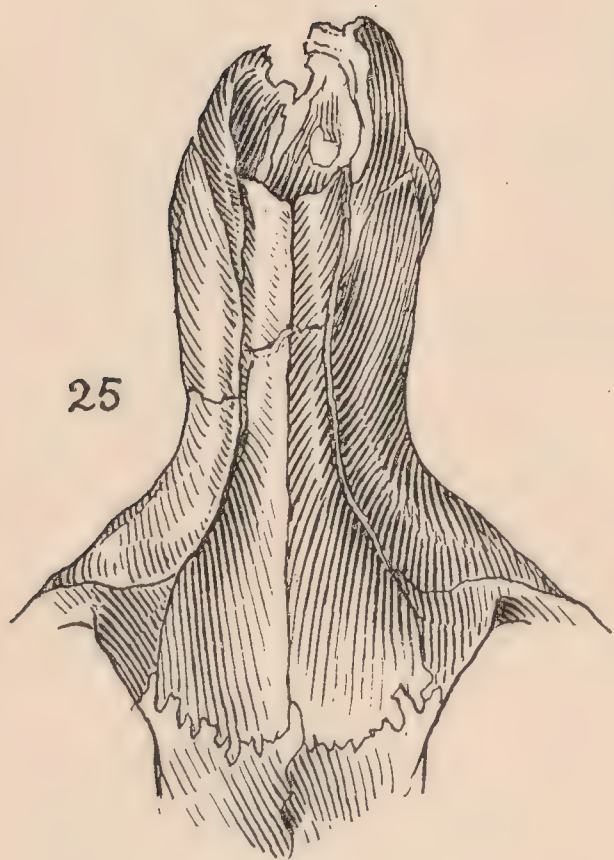
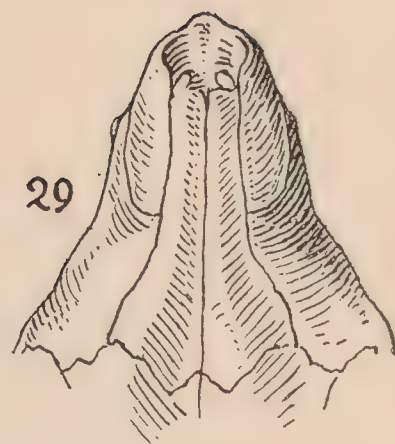
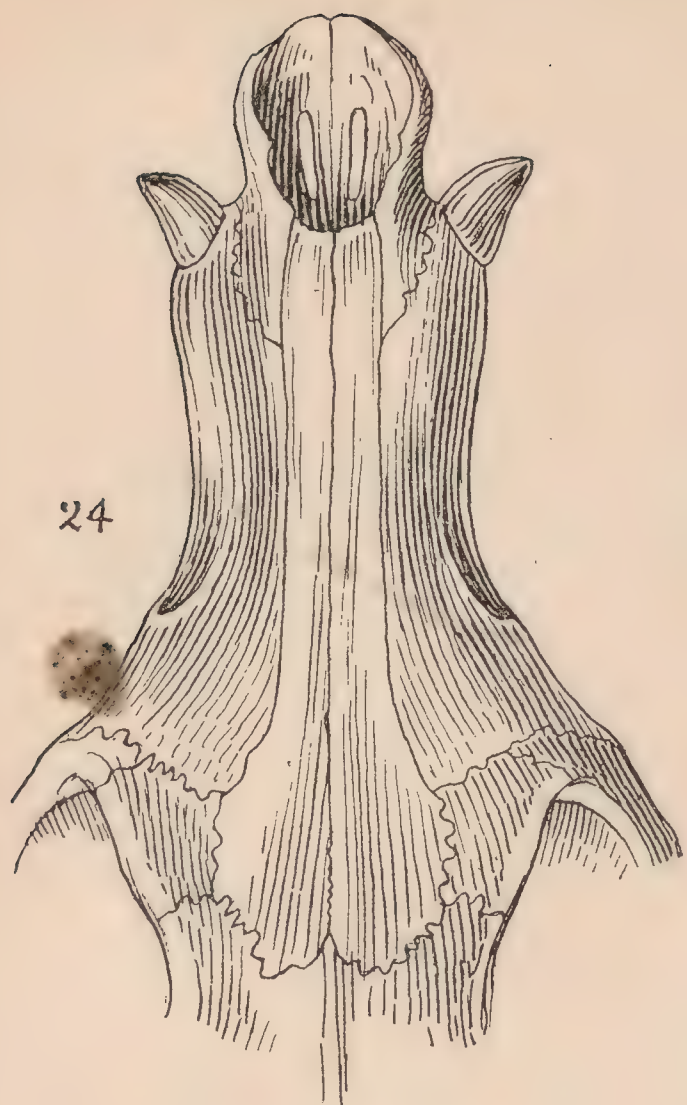
- Fig. 1. *Philander* sp. No. 2072. $\times 4$.
 Fig. 2. *Metachirus* sp. No. 244. $\times 2$.
 Fig. 3. *Caluromys derbianus*. No. 10058. $\times 2$.
 Fig. 4. *Chironectes minimus*. No. 33027. $\times \frac{3}{2}$.
 Fig. 5. *Marmosa chapmani*. No. 4773. $\times 3$.
 Fig. 6. *Didelphys virginiana*. No. 242. $\times \frac{5}{4}$.
 Fig. 7. *Borhyæna tuberata*. Princeton Univ. No. 15701. (After Sinclair.) $\times 1$.
 Fig. 8. *Prothylacinus patagonicus*. P. U. No. 15700. (After Sinclair.) $\times 1$.
 Fig. 9. *Cladosictis lustratus*. P. U. No. 15170. (After Sinclair, lower teeth reversed.) $\times 1$.
 Fig. 10. *Amphiproviverra mazaniana*. No. 9254. $\times 1$.
 Fig. 11. *Thylacinus cynocephalus*. No. 35504. $\times 1$.
 Fig. 12. *Dasyurus viverrinus*. No. 16669. $\times 1$.
 Fig. 13. *Sarcophilus ursinus*. No. 35106. $\times 1$.
 Fig. 14. *Phascogale cristicaudata*. No. 15009. $\times 2$.
 Fig. 15. *Antechinomys laniger*. No. 15012. $\times 2$.
 Fig. 16. *Sminthopsis crassicaudata*. No. 15013. $\times 2$.



- Fig. 17. *Philander* sp. No. 2702. $\times 2$.
Fig. 18. *Metachirus* sp. No. 244. $\times 1$.
Fig. 19. *Caluromys derbianus*. No. 10058. $\times 1$.
Fig. 20. *Chironectes minimus*. No. 33027. $\times 1$.
Fig. 21. *Marmosa chapmani*. No. 4773. $\times 2$.
Fig. 22. *Didelphys virginiana*. No. 240. $\times 1$.
Fig. 23. *Borhyæna tuberata*. P. U. No. 15701. (After Sinclair.) $\times 1$.

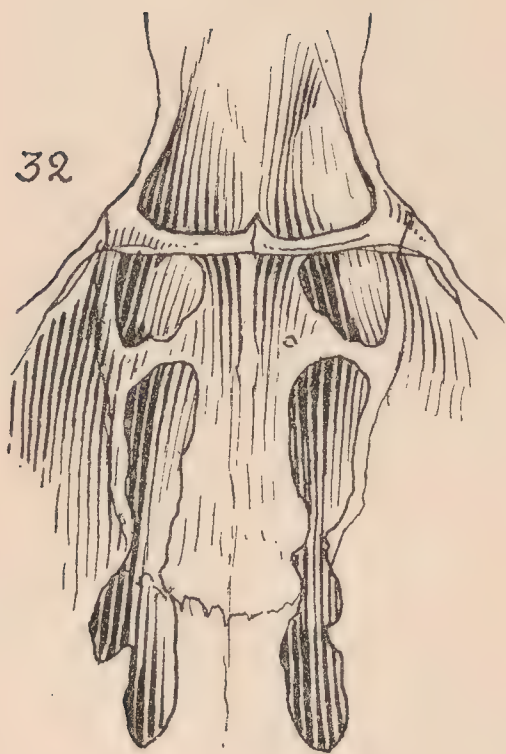


- Fig. 24. *Cladosictis lustratus*. P. U. No. 15046. (After Sinclair.) × 1.
Fig. 25. *Amphiproviverra mazaniana*. No. 9254. × 1.
Fig. 26. *Thylacinus cynocephalus*. No. 35504. × 1.
Fig. 27. *Dasyurus viverrinus*. No. 16669. × 1.
Fig. 28. *Sarcophilus ursinus*. No. 35106. × 1.
Fig. 29. *Phascogale cristicaudata*. No. 15009. × 2.
Fig. 30. *Antechinomys laniger*. No. 15012. × 2.
Fig. 31. *Sminthopsis crassicaudata*. No. 15013. × 2.

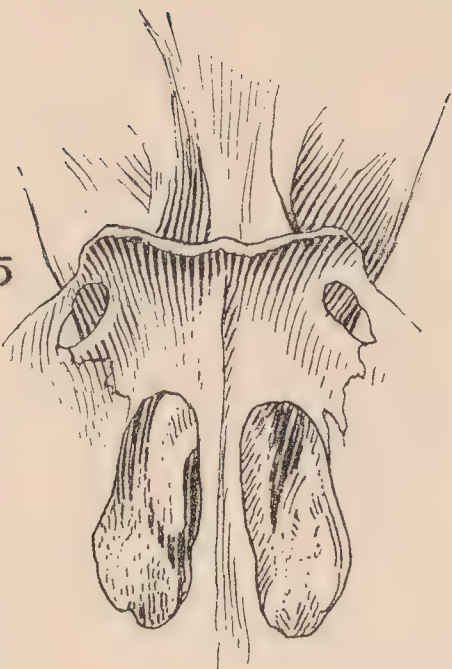


- Fig. 32. *Philander* sp. No. 2072. $\times 4$.
Fig. 33. *Metachirus* sp. No. 244. $\times 2$.
Fig. 34. *Caluromys derbianus*. No. 10058. $\times 2$.
Fig. 35. *Chironectes minimus*. No. 33027. $\times \frac{3}{2}$.
Fig. 36. *Marmosa chapmani*. No. 4773. $\times 3$.
Fig. 37. *Didelphys virginiana*. No. 240. $\times \frac{5}{4}$.
Fig. 38. *Borhyæna tuberata*. P. U. No. 15701. (After Sinclair.) $\times 1$

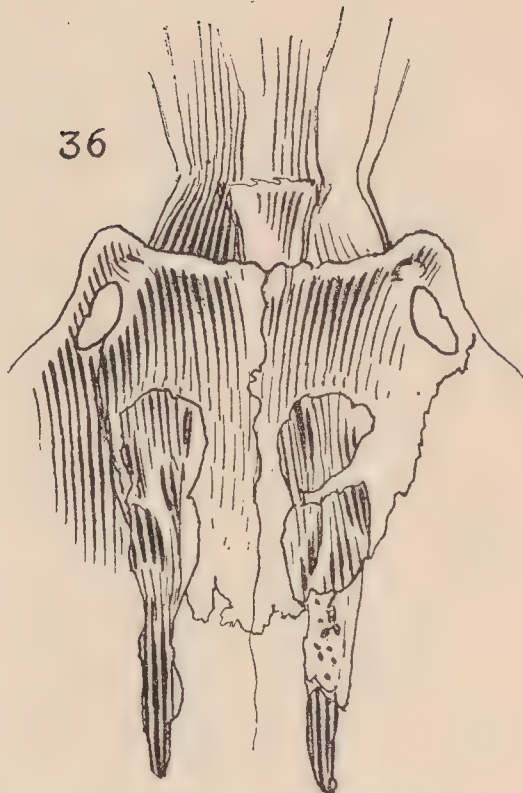
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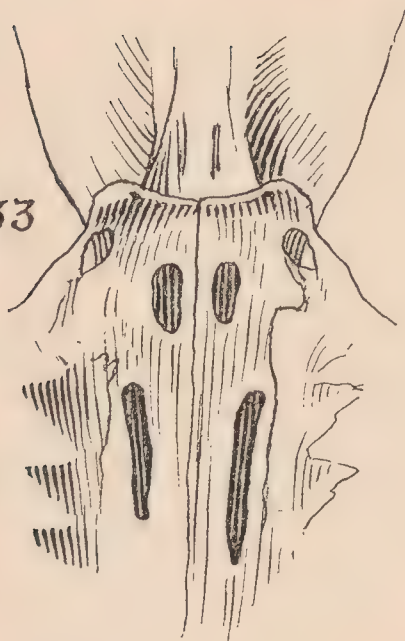
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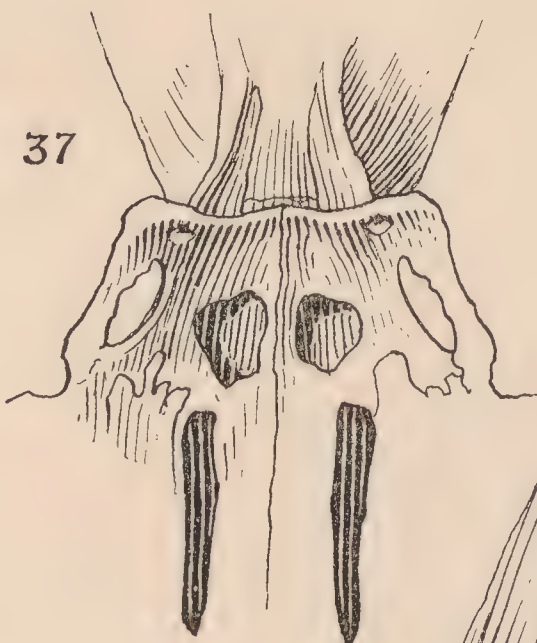
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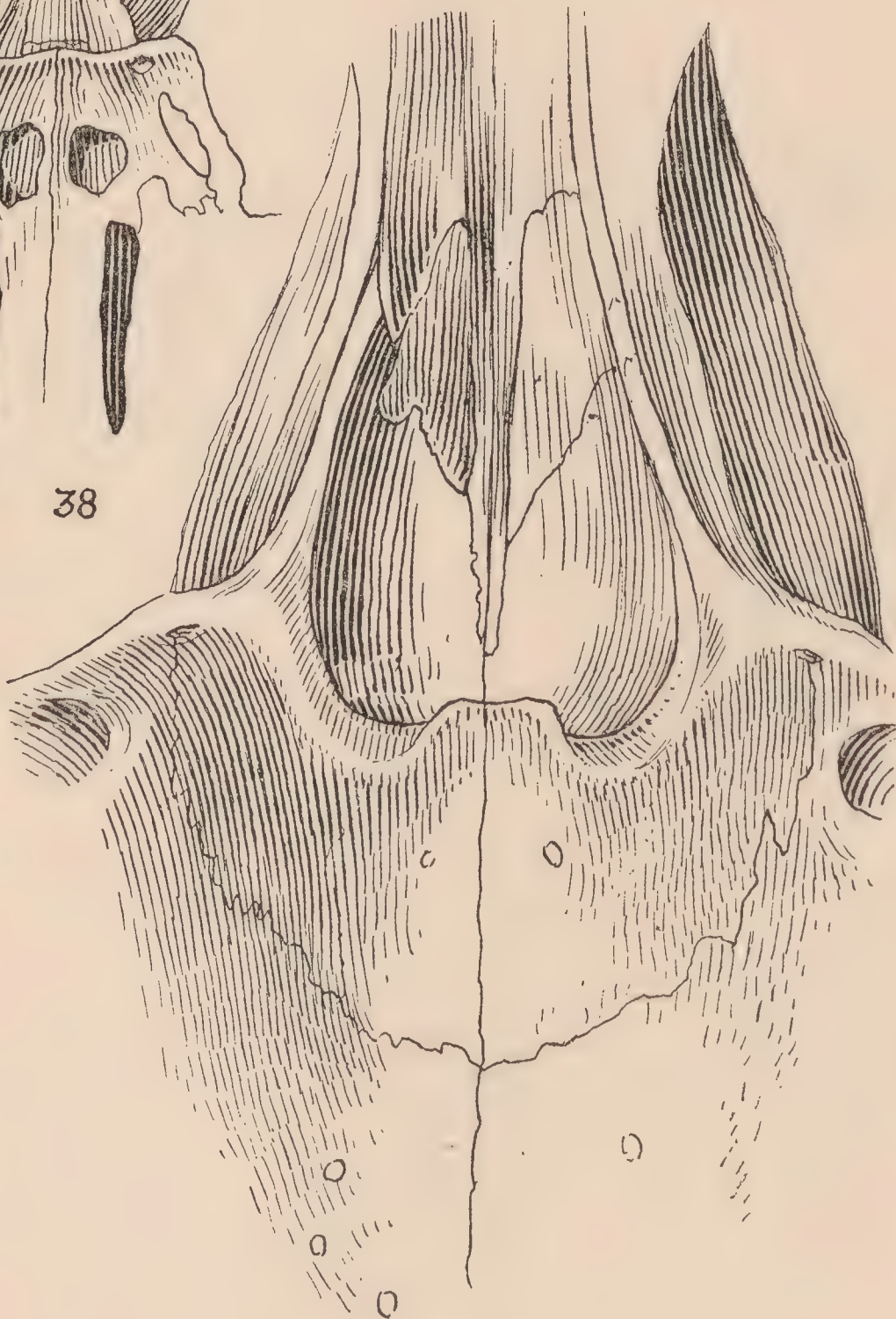
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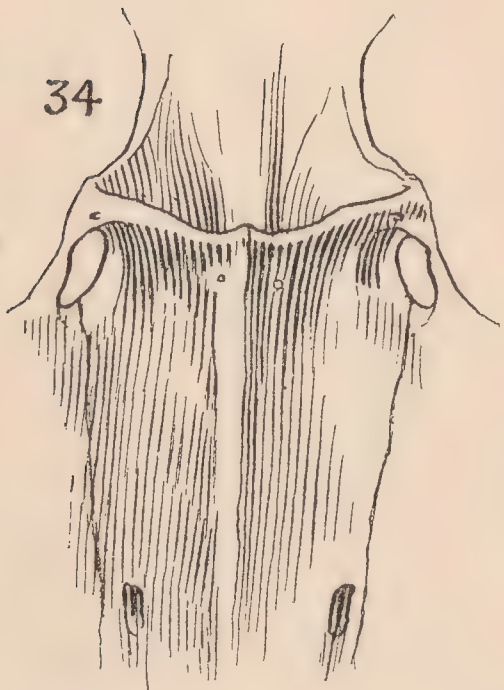
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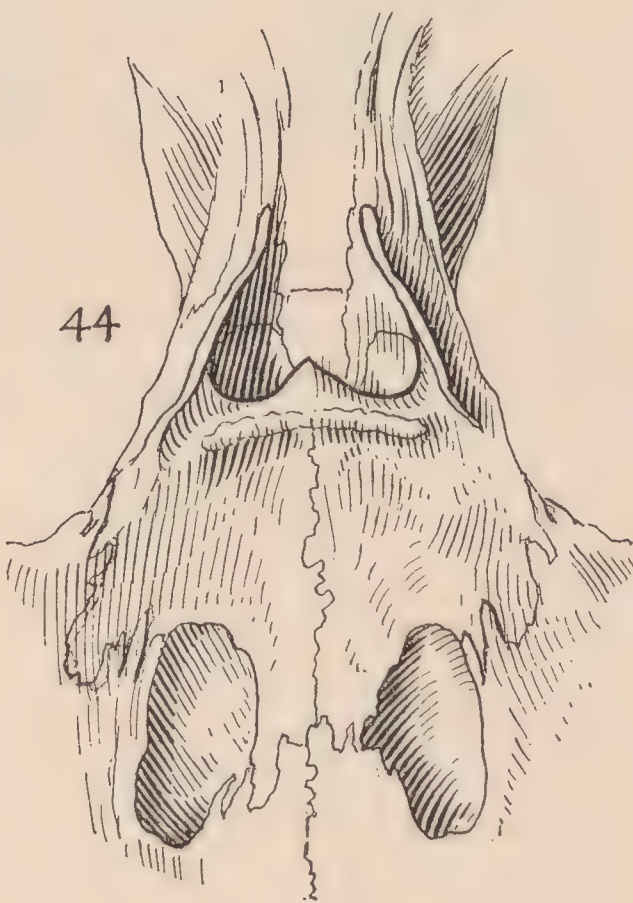
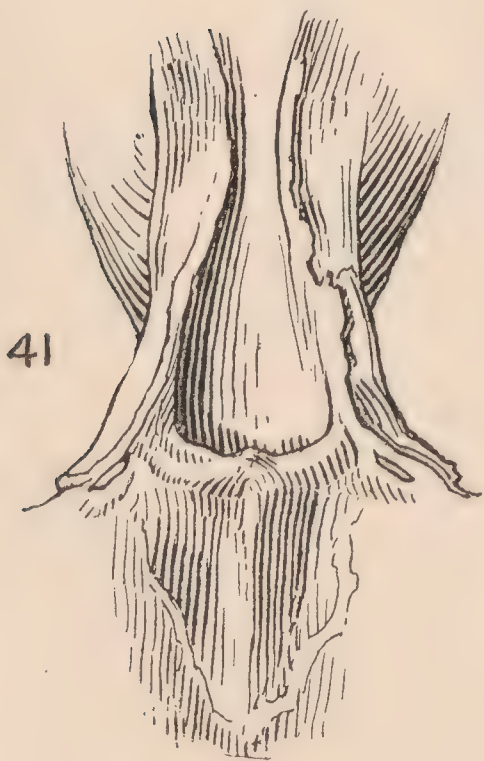
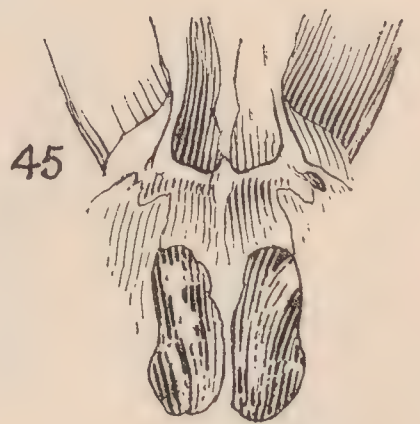
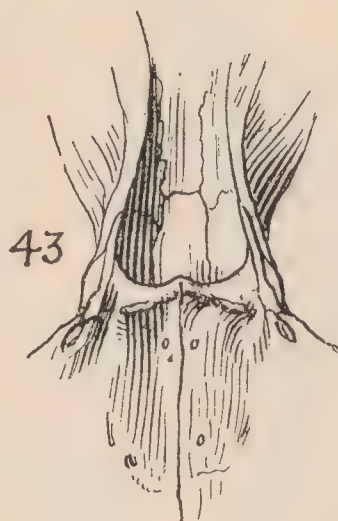
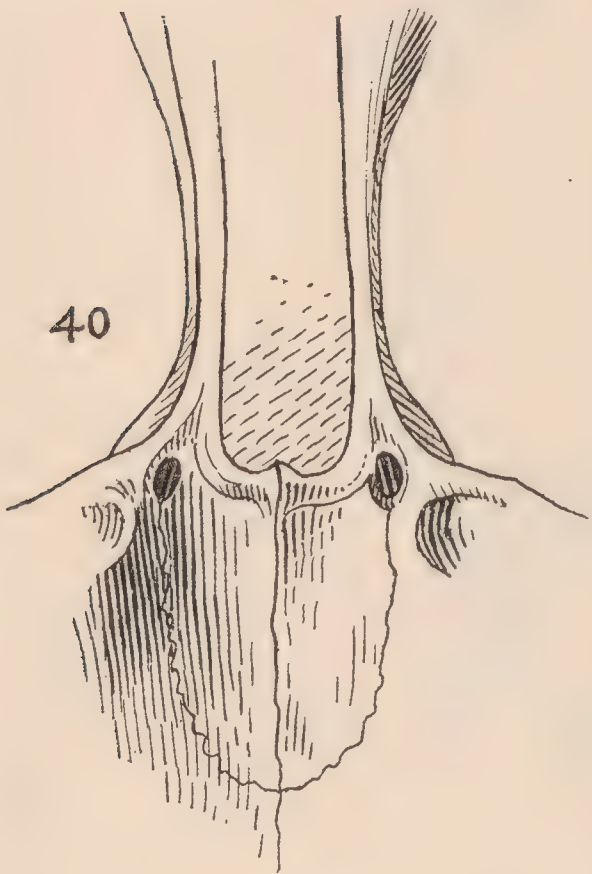
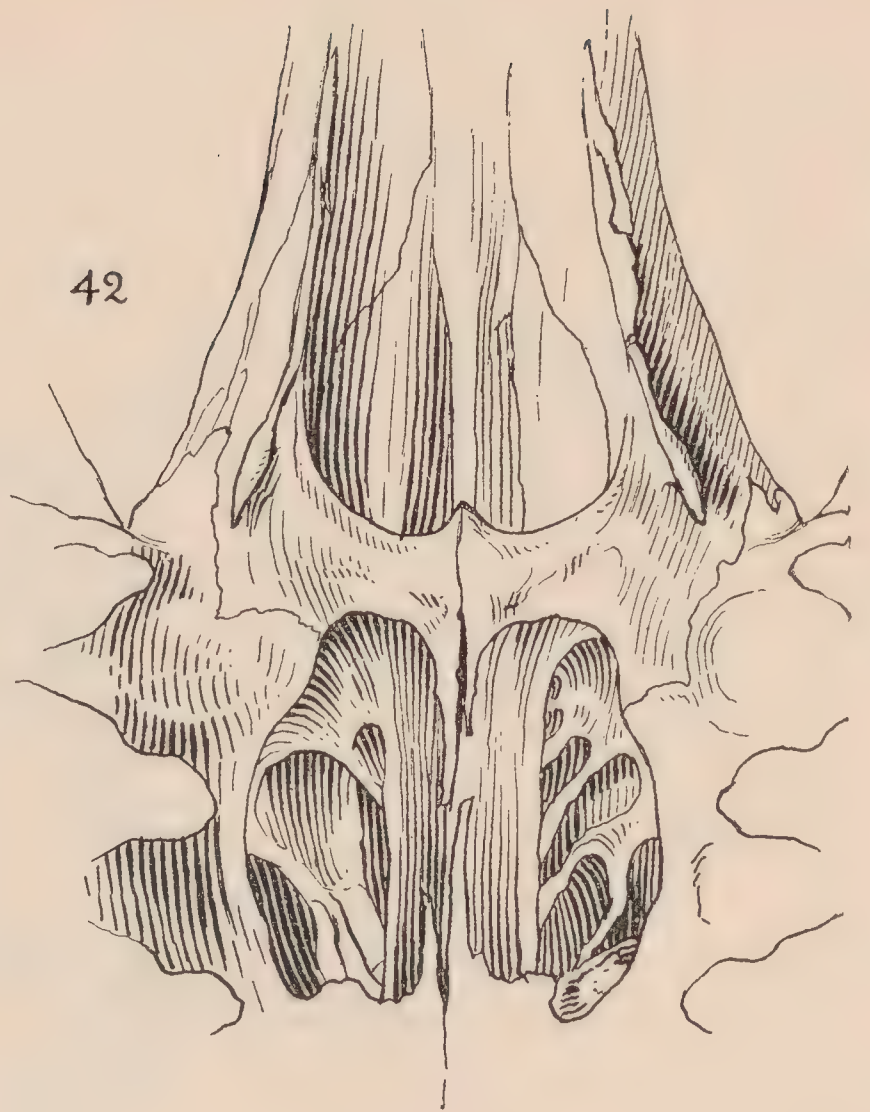
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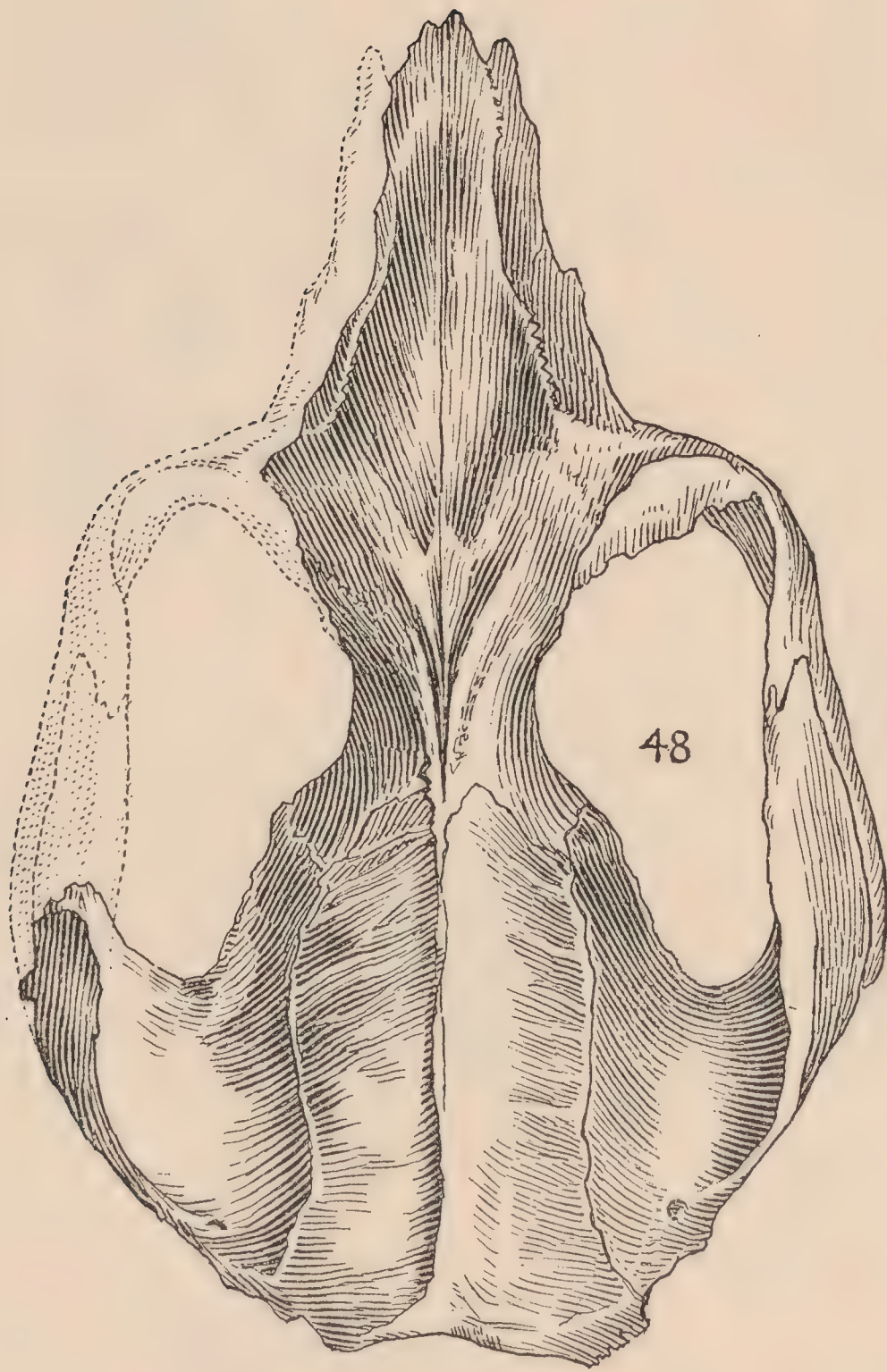


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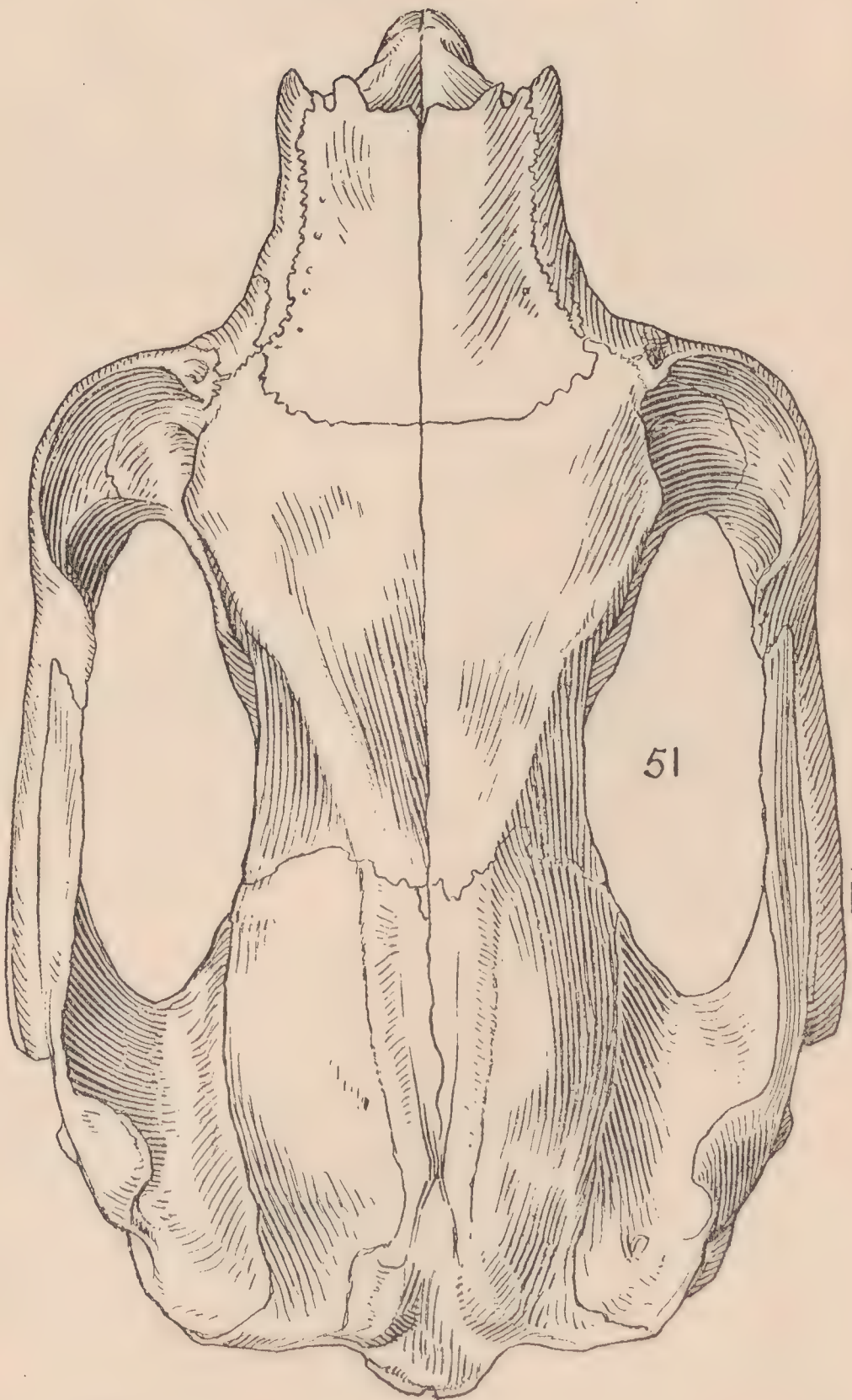
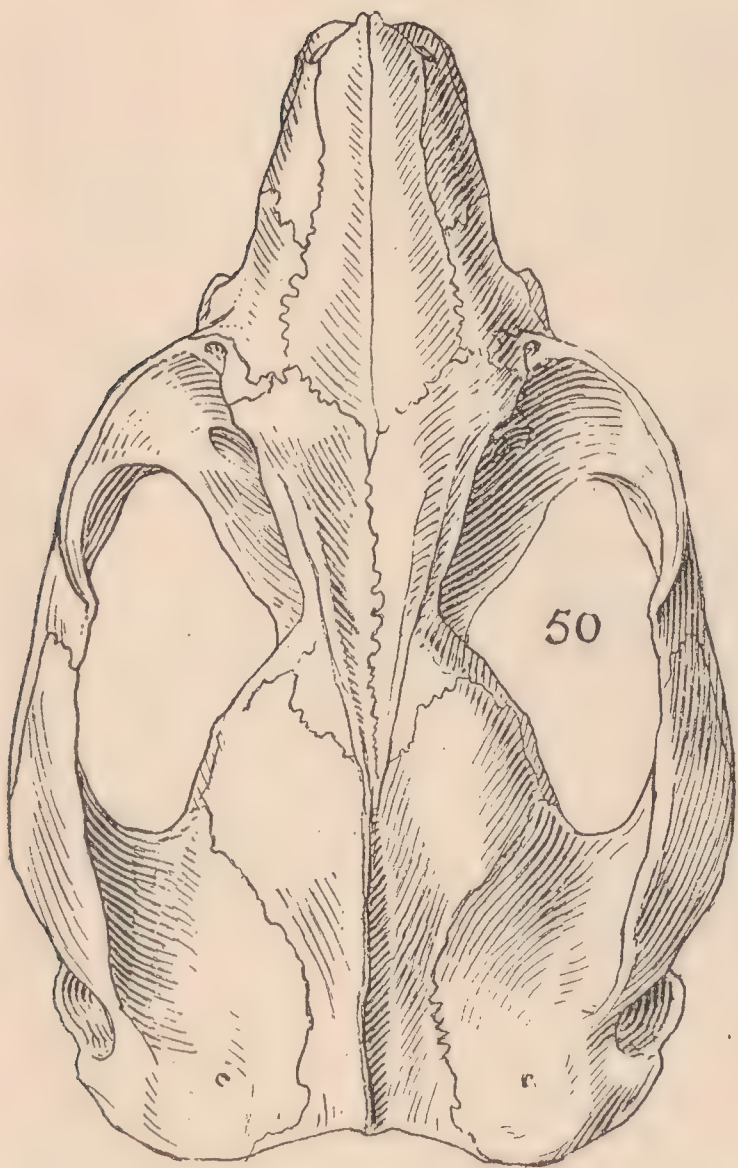
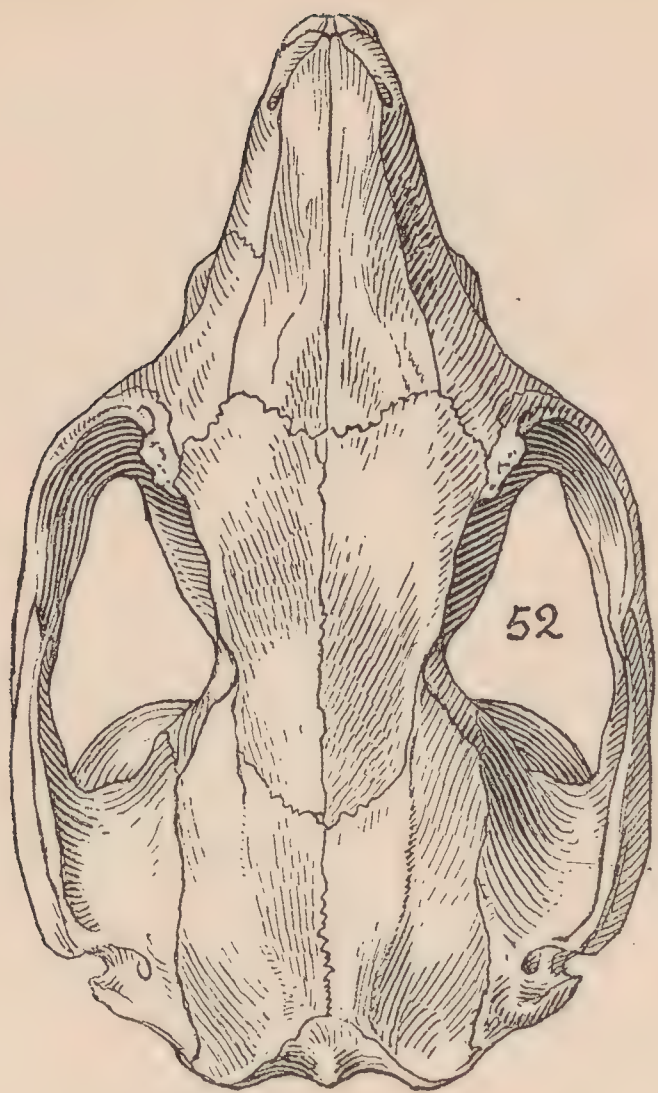
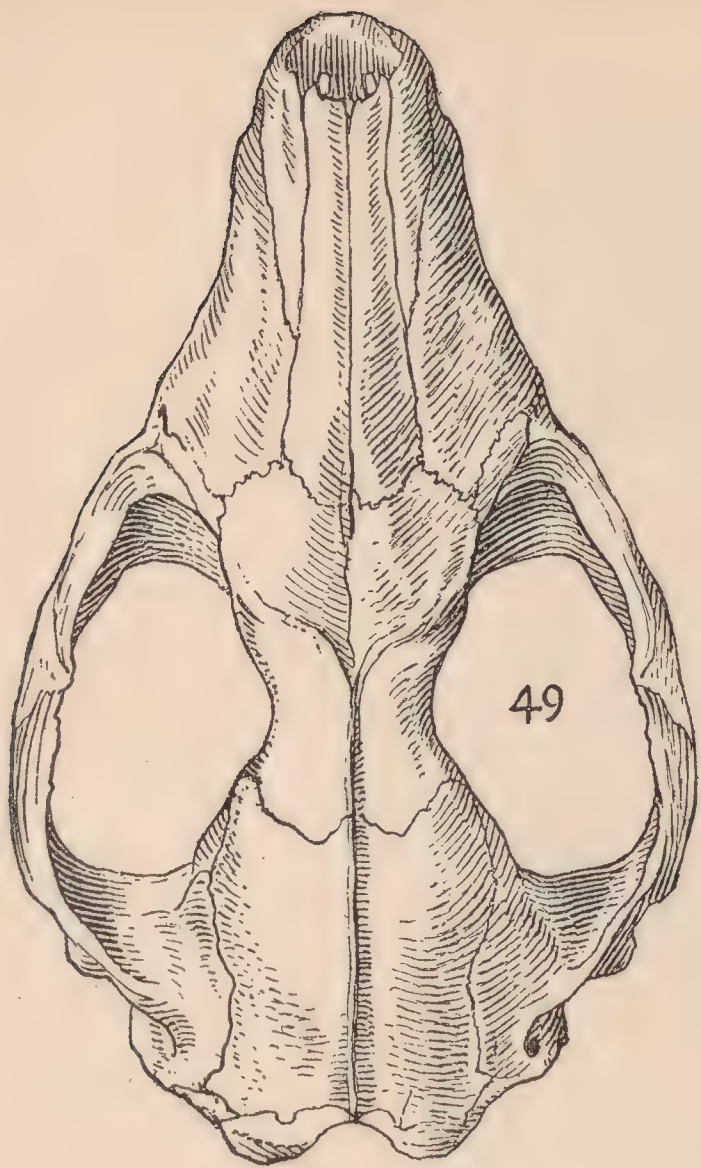


- Fig. 39. *Prothylacinus patagonicus*. P. U. No. 15700. (After Sinclair.) × 1.
 Fig. 40. *Cladosictis lustratus*. P. U. No. 15046. (After Sinclair.) × 1.
 Fig. 41. *Amphiproviverra mazaniana*. No. 9254. × 1.
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 Fig. 43. *Dasyurus viverrinus*. No. 16669. × 1.
 Fig. 44. *Sarcophilus ursinus*. No. 35106. × 1.
 Fig. 45. *Phascogale swainsoni*. Raven Coll. 91. × 2.
 Fig. 46. *Antechinomys laniger*. No. 15012. × 2.
 Fig. 47. *Sminthopsis crassicaudata*. No. 15013. × 2.

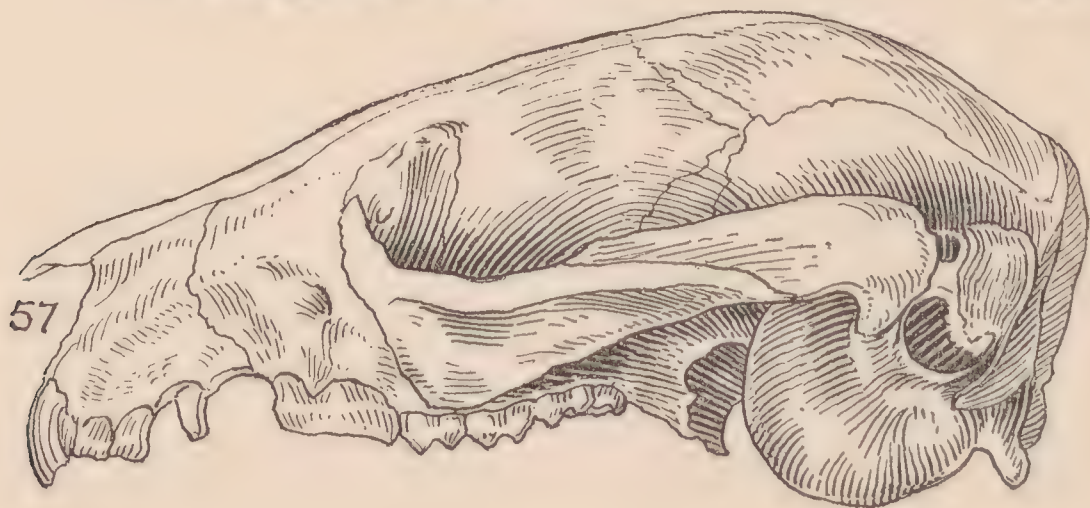
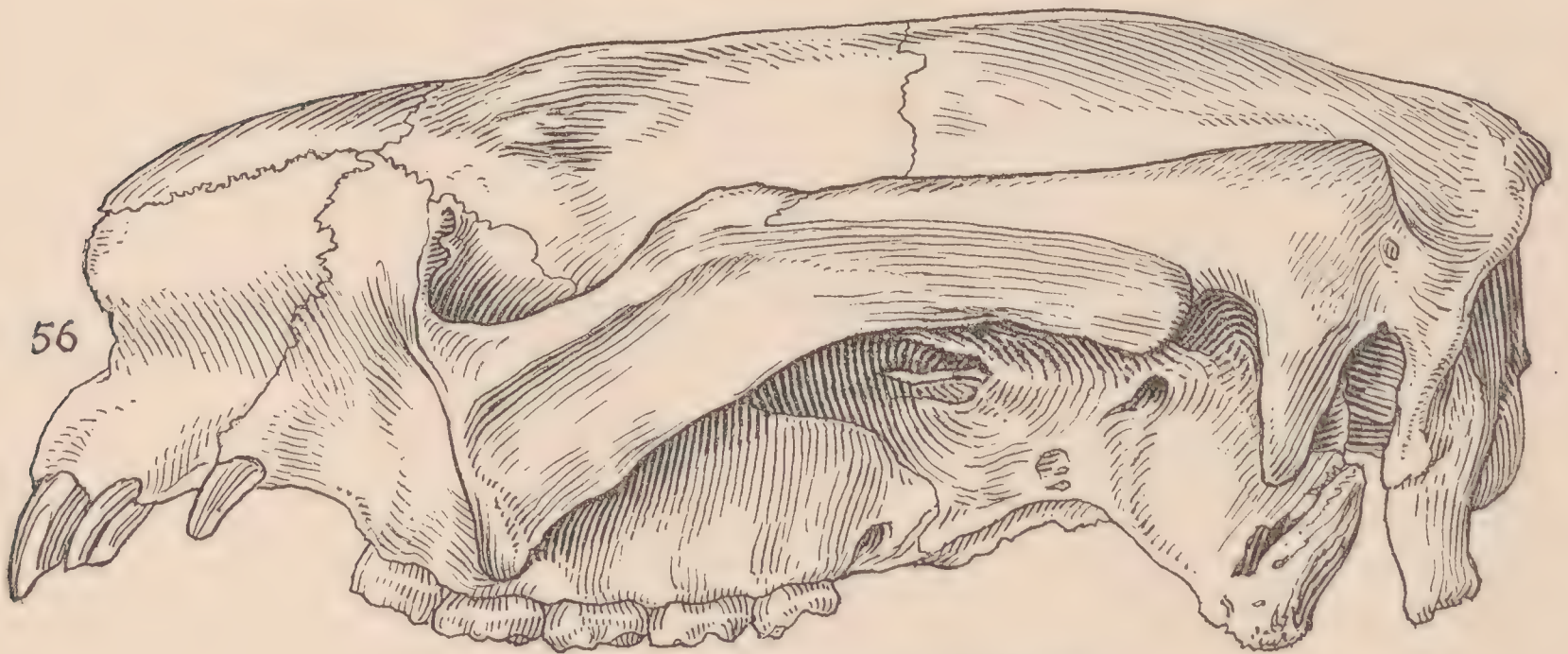
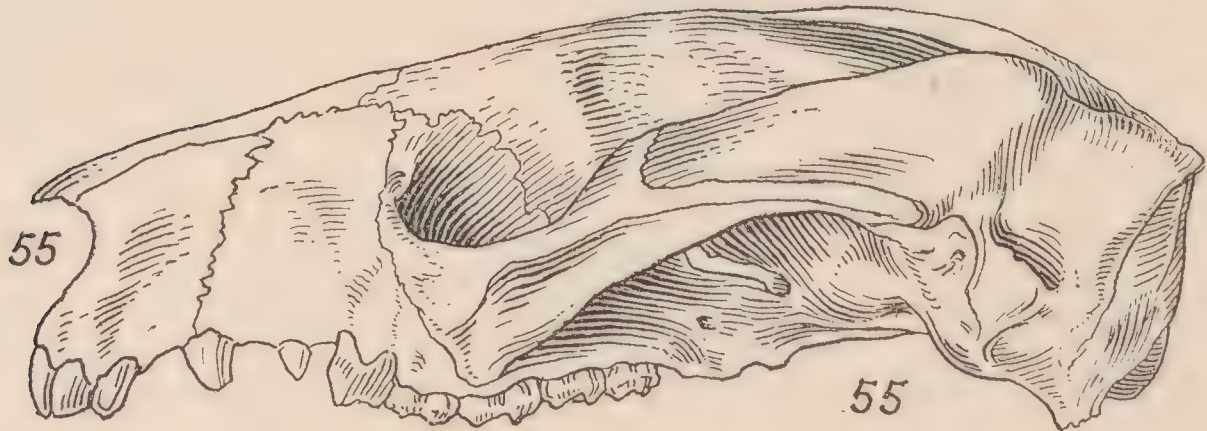
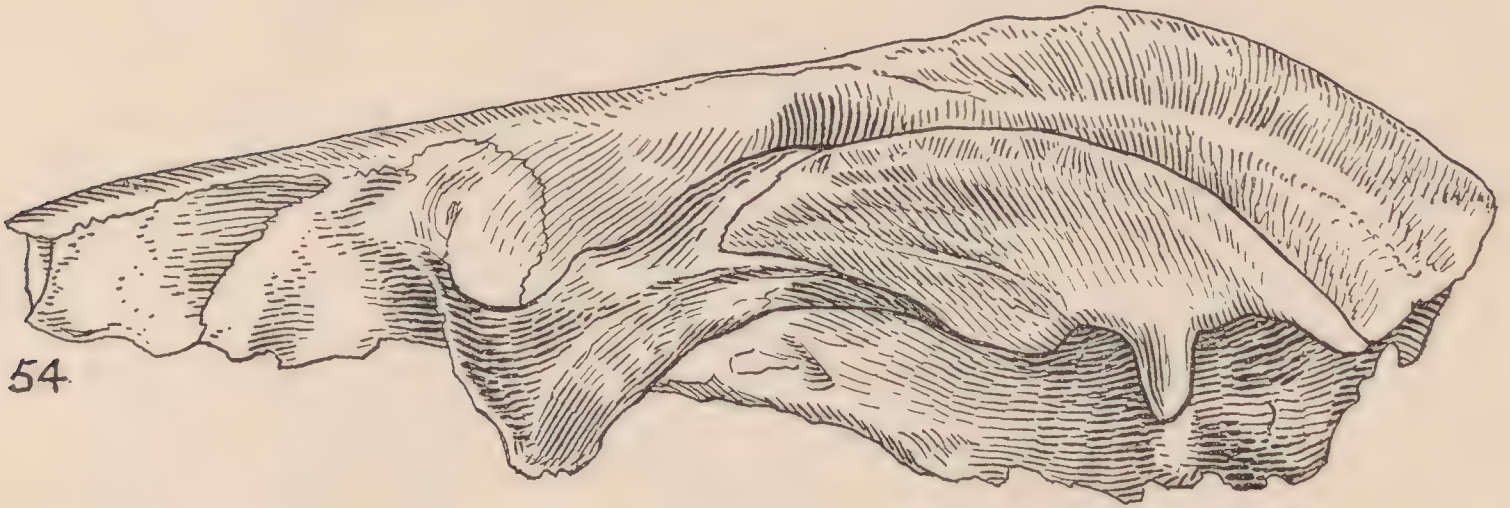
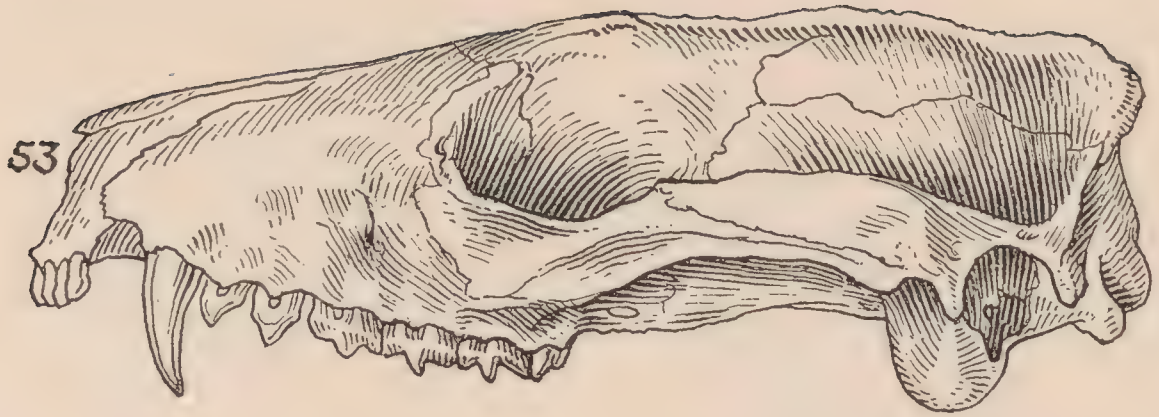




- Fig. 48. *Wynyardia bassiana*. (After Spencer.) $\times 1$.
 Fig. 49. *Dasyurus viverrinus*. No. 16669. $\times 1$.
 Fig. 50. *Trichosurus vulpecula*. No. 249. $\times 1$.
 Fig. 51. *Phascolarctus cinereus*. No. 42178. $\times 1$.
 Fig. 52. *Bettongia* sp. No. 6364. $\times 1$.



- Fig. 53. *Dasyurus viverrinus*. No. 16669. $\times 1$.
Fig. 54. *Wynyardia bassiana*. (After Spencer, reversed.)
Fig. 55. *Trichosurus vulpecula*. No. 249. $\times 1$.
Fig. 56. *Phascolarctus cinereus*. No. 42178. $\times 1$.
Fig. 57. *Bettongia* sp. No. 6364. $\times 1$.



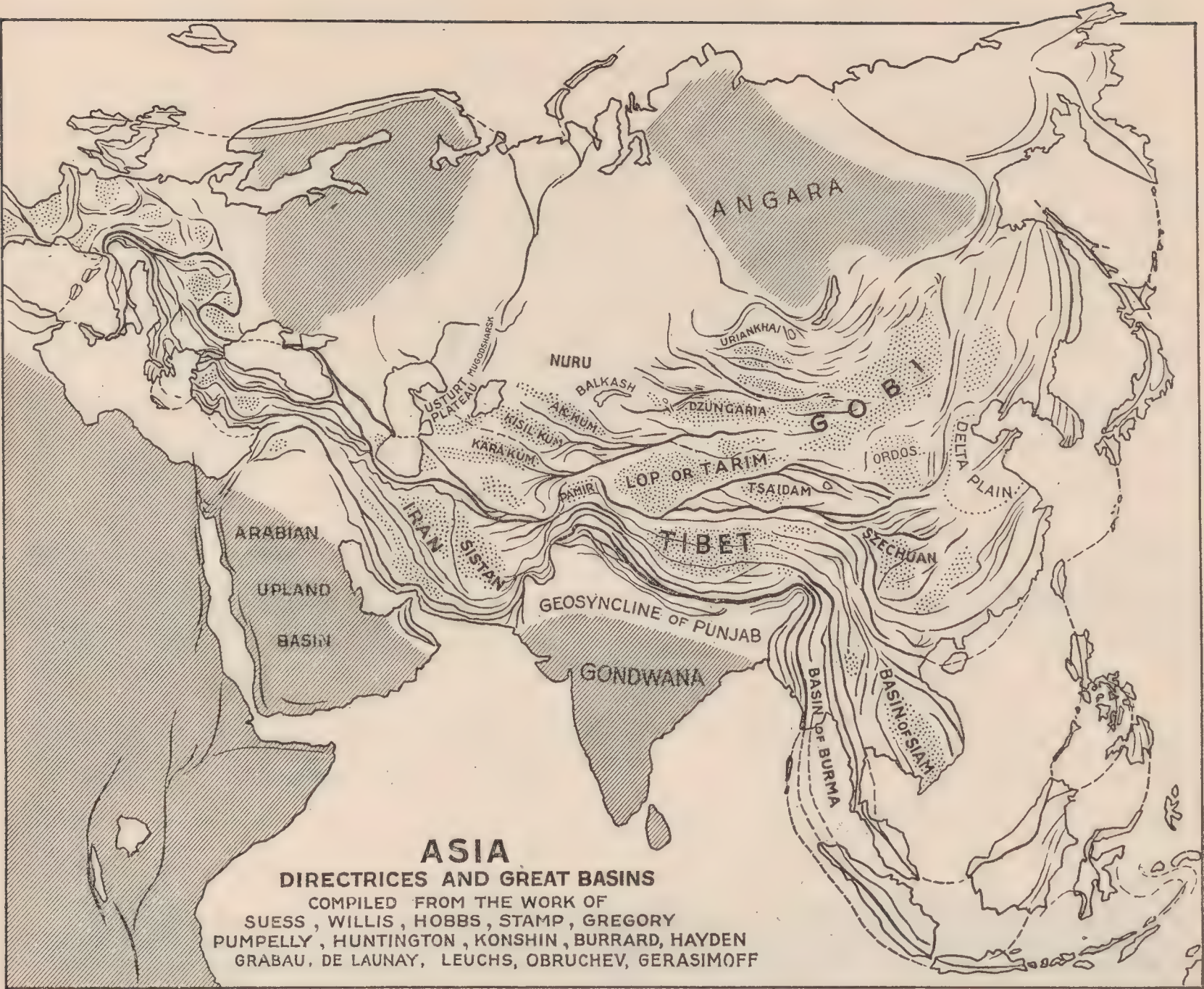


Fig. 1. Map of Asia, showing the trend of mountain ranges, and the position of the great basins.
Large positive elements are shaded in slanting lines. The great structural basins are stippled.

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Article V.—BASIN STRUCTURES IN MONGOLIA¹

BY CHARLES P. BERKEY AND FREDERICK K. MORRIS

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¹Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 29.

INTRODUCTION

Between the vast areas of Asia enjoying ocean drainage lies a series of great interior basins of diverse type, extending from the Amur headwaters in the northeast to the Caspian in the southwest; and from the Arctic divide to the Himalayas. These basins, as indicated on the accompanying map (Fig. 1), are the Gobi, the Dzungaria (or Sinkiang), the Lop (Tarim or Taklamakan), the Balkash and Aral-Caspian, besides high intermontane basins like Tibet and Iran. All these are semiarid steppe-countries, including desert ranges, broad, open minor basins, and occasional depressions with lakes and salt pans.

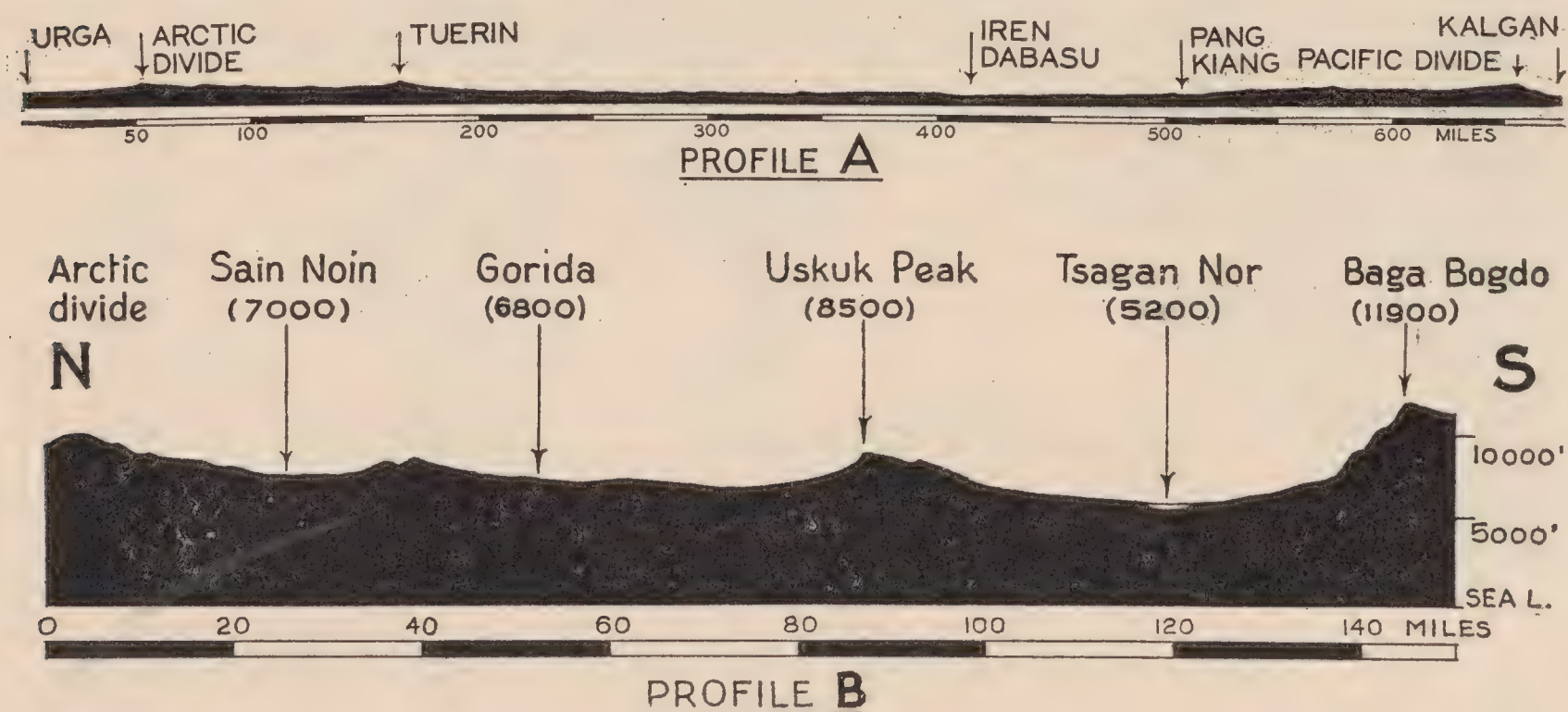


Fig. 2A. Profile across the Gobi region between Kalgan and Urga, showing a broad, very shallow downwarp between the Arctic and Pacific divides. Vertical scale $\times 10$.

B. Profile across the northern part of the Gobi region, between the Khangai and Altai mountain ranges, showing stronger warping and block-faulting in this part of the great basin than in the eastern section. Vertical scale $\times 10$.

The Gobi, easternmost of the great basins, has a width of, roughly, 500 miles north and south; and a length of 1,000 miles east and west. The entire country from the southerly margin to the Arctic divide is warped into a gently sloping concavity, or broad open syncline, whose central portion is 3,000 feet lower than the outer margins. Thus the rims of the basin stand from 5,000 to 7,000 feet above the sea, and the broad, downwarped expanse between forms a basin-shaped plateau, parts of which are real desert. Generalized profiles are plotted in figure 2. We judge that the eastern profile represents almost pure warping, while the western profile is the result of warping plus extensive faulting in the midst of the original basin.

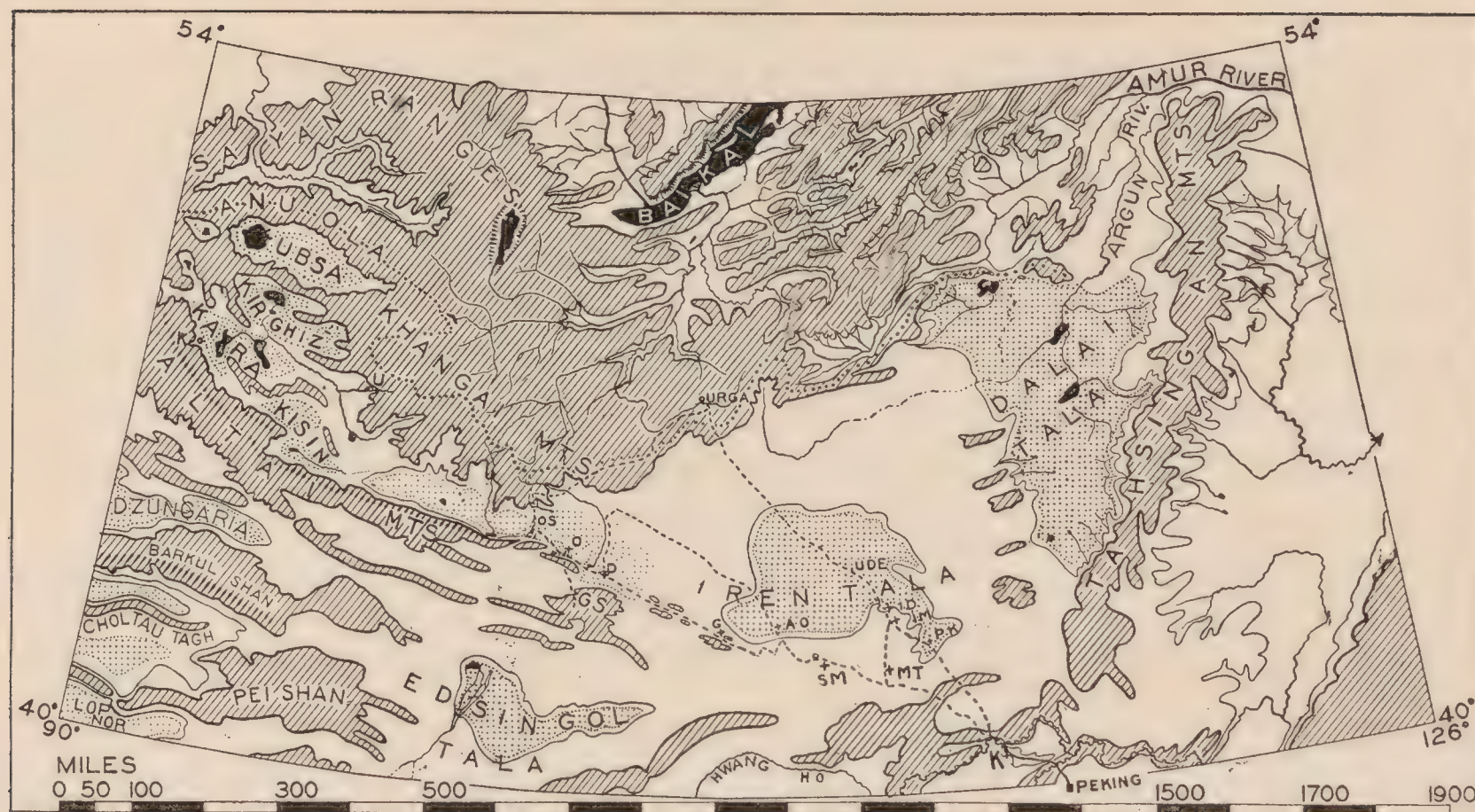


Fig. 3. Map of the Gobi region.

The mountainous areas are shaded with slanting lines. The lowlands are white, while the deeper depressions are stippled. This map serves as a location map for the talas named in the text, and also shows the routes of the Expedition. The index-letters have the following meanings: AO, Ardyn Obo; D, Djadochta; G, Golobai; GS, Gurbun Saikhan; ID, Iren Dabasu; IM, Irdin Manha; K (northwest of Peking), Kalgan; K (in the west, just north of the initial A of ALTAI), Kobdo; MT, Murukh Tchu; O, Oshih (Ashile); OS, Ondai Sair; PK, Pang Kiang; SM, Shara Murun; U (south of the K of KHANGAI), Uliassutai.

The great basin of the Gobi contains many minor basins, which we are calling "talas," from a Mongol word for an open steppe-country (Fig. 3). The following talas may be demonstrated: the Dalai Nor tala, now draining through the Argun river to the Amur; the Iren tala; the Gashuin Nor, or Edsin Gol tala; the Kisin or Shargin tala; the Khara and Dzapkhin, or Kirghiz Nor tala, in which are the cities of Kobdo and Uliassutai; the Tez, or Ubsa Nor tala. Each tala has its own local interior drainage and is bounded by inconspicuous warp divides or by mountain ranges, or both, separating it from neighboring areas of similar habit.

Again, within each tala there are still smaller basins, which contain sediments of late Mesozoic or Tertiary age, or both. These smaller units appear as broad level spaces whose surface is beveled by the Gobi peneplane, the remarkably smooth flat surface of which is one of the most striking features of Mongolia. These basins of the third order of magnitude are the units of special interest to this investigation. Inquiring of the Mongols as to the derivation of the word "gobi," it was found that such open level-surfaced basins are called "gobis," and we can think of no better term by which to call them in science. A cross section taken from one of the field books will serve to show the typical structure of such a minor basin, or gobi, in a restricted sense (Fig. 4).

NATURE OF THE ROCK FLOOR

The oldrock floor is a complex of ancient sedimentary strata, metamorphic rocks and intrusive igneous masses, both large and small. The oldest rocks recognized by us are complex injection-gneisses, crystalline limestones and related rock types exhibiting the most complex structural conditions and mixtures of composition found in the whole region. They appear to be more deformed, more modified, and richer in injected igneous material than any of the other series, and they are the most confusing to interpret. They should be the oldest of all and may indeed correspond to the Archæan of other lands. On these grounds they are judged to be Archæan, and to represent the T'ai Shan complex described by Willis and Blackwelder as occurring in China proper.¹

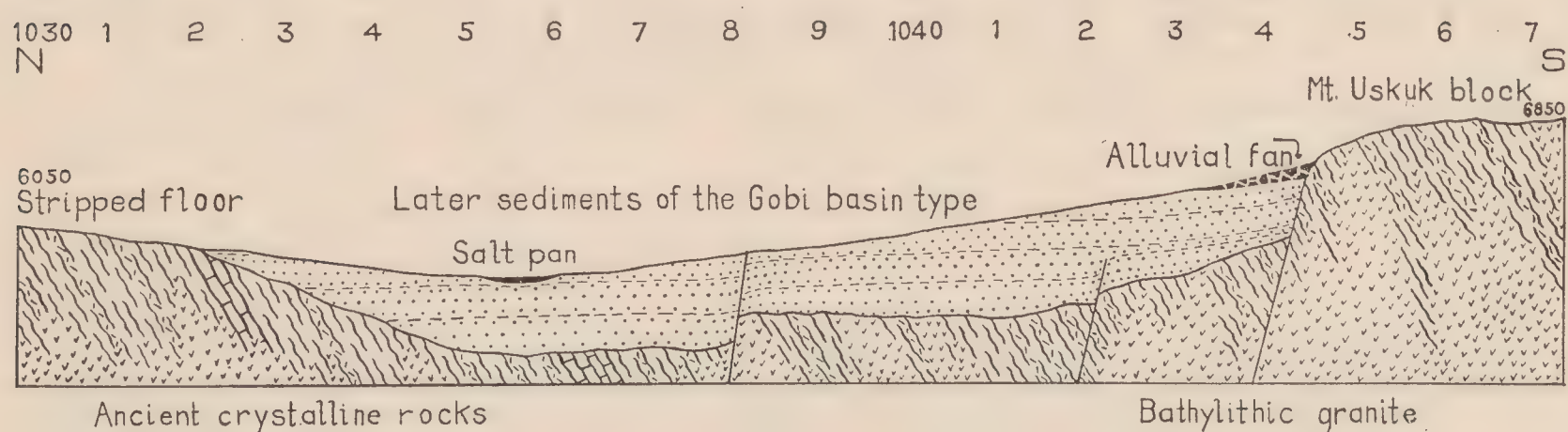


Fig. 4. Cross section from the geologist's field notebook, showing the basin north of Uskuk Mountain.

Ancient crystalline rocks—gneisses, schists and interbedded limestones, invaded by granites representing the Great Mongolian Bathylith, form the warped floor on which later sediments have been accumulated. Further deformation with faulting has affected the basin, pushing up the Mt. Uskuk block and making possible development of alluvial fans. Erosion has stripped some of the floor and has carved a broad shallow valley in the sediment, in the almost abandoned depressions of which a salt pan is located. This section is almost continuous with Fig. 10, which lies south of the Uskuk block.

The next younger series includes schists and crystalline limestones which are found in the Tsetsenwan hills. Between Shara Murun and Ardyn Obo, there is a great series of greenstones and phyllites which we consider to be older than the Khangai graywackes next to be described. The fact that these series have not been observed in close contact with one another makes it difficult to determine their exact relations. They are very clearly more intensely modified by metamorphic processes and constitute a more varied series than does the graywacke series referred to as the Khangai, and they evidently belong to a more ancient geologic time. Perhaps the early Proterozoic system, the Wu T'ai Shan, as used in China, is large enough to hold them.

¹Willis, Bailey, Blackwelder, Eliot, and Sargent, R. H. 1907. "Research in China," I, pp. 19, 59, 99, 157; II, p. 1; Carnegie Institution of Washington, Pub. 54.

The most widespread sedimentary unit was given the field name "Khangai series," from a range of mountains of that name on the Arctic divide. The total thickness of the series is not less than 20,000 feet. It consists almost wholly of graywackes, siliceous argillites and slates. Locally, red jasper or blue siliceous limestone is found with these strata, but these types do not figure heavily in the series as a whole. The rocks are not very highly metamorphosed, and yet they are surprisingly unfossiliferous. The immense extent, great thickness and uniform character of this formation are most impressive. The strata are everywhere strongly folded, and because of the lack of fossils, together with the general structural relations, are judged to be late pre-Cambrian—possibly to be correlated with the Nan K'ou of Richthofen and Bailey Willis,¹ or the Sinian of Grabau,² as described for China.

Besides many minor intrusive bodies, all these series of rocks are cut by an immense bathylith, dominantly granite, the great stocks of which are exposed over broad areas. Apophyses from it were found as far north as the Khangai range and the Gangin Daba and Olon Obo mountains, and it is our belief that the granite of Nan K'ou Pass above Peking belongs to the same unit. Possibly this bathylith is genetically responsible for the mineralization of the gold veins north of Urga and in the Ulias-sutai country.

Overlying these formations unconformably are marine limestones, limy shales and sandstones with fossils of Mississippian, possibly of Pennsylvanian, and certainly of Permian age. All are very complexly folded and faulted and have been almost completely swept away in the course of later erosions. Only two comparatively small infolded synclinal and graben-fault remnants of the sedimentary formations of this short-lived, but significant, Paleozoic geosyncline were found in Mongolia. A few dikes cut these beds, but no large intrusives seem to have reached them.

Unconformable, also, upon the pre-Paleozoic rocks, is an extensive and persistent series of continental conglomerates, sandstones and minor shales, with interbedded tuffs and surface flows, the aggregate thickness of which is in places more than 10,000 feet. Obscure woody plant-remains are found in these coarse clastics, and at one locality several thin seams of coal were seen. All are strongly folded and the question may be raised whether the same disturbance folded these that plicated the marine

¹von Richthofen, Ferdinand Freiherr. 1882. "China," II, pp. 316-317, Berlin. Willis, Bailey, Blackwelder, Eliot, and Sargent, R. H. 1907. "Research in China," I, p. 123, Carnegie Institution of Washington, Pub. 54.

²Grabau, A. W. 1922. "The Sinian System," Bull. Geol. Soc. China, I, p. 44.

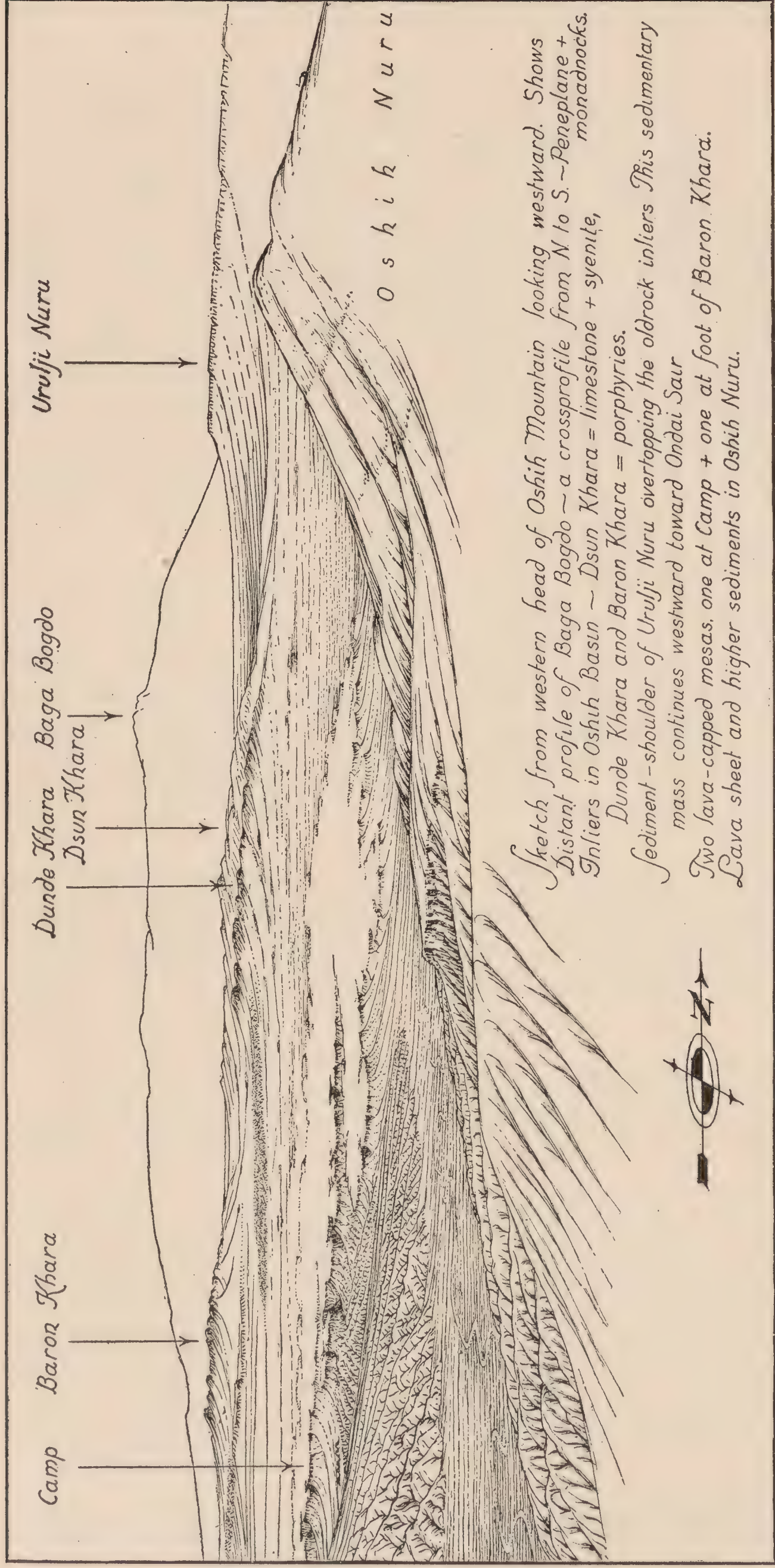


Fig. 5. Sketch in the Oshih basin, looking westward.

Baga Bogdo, seen in profile from north to south, shows the narrowness of the Altai range in this dimension. Two low ranges of hills in the middle distance consist, the one of folded trachyte porphyry, and the other of crystalline limestone, cut by syenite. The high shoulder at the right, called Urulji Nuru, represents sediments that once extended over the hard-rock ridges. At the foot of these ridges are two areas of badlands, the southern one capped by a lava sheet. The lava reappears in the broad mesa in the center of the sketch. A fault runs along the nearer front of this mesa, and the edge of the lava bends notably downward toward the spectator. The edge of the faulted lava sheet reappears in Oshih Mountain in the extreme foreground. The sketch emphasizes the unevenness of the old floor and the enormous amount of sediment that has been stripped from it.

Paleozoic beds. At another time, we may submit evidence for the view that the two series were folded at different times and that the conglomerate series is approximately of the same age as the folded coal-bearing conglomerates and shales of northern China, which are conceded to be of Lower Jurassic age. The latest mountain-folding, then, follows the development of these Jurassic strata and, if this correlation proves admissible, must be of Middle or late Jurassic date.

At this point in the geologic column, a complete change of structural behavior takes place. All earlier rocks are mountain-folded and extensively deformed, whereas those strata that lie above them are not folded at all, and, although they are tilted and warped, or broken, they are only locally much deformed even in this way. The Jurassic unconformity marks, therefore, the most significant break in the whole geologic column for central Mongolia. It marks the change from repeated deformative revolutions to a state of much greater stability and the establishment of a continental history that has persisted unbroken to the present day.

BASIN SEDIMENTS

All these older disturbed rocks were worn down to a mature, rolling, locally baseleveled surface before the first of the nearly horizontal sediments in which we find vertebrate fossils was laid down. A sketch (Fig. 5) made in the Oshih (Ashile) basin, oldest of the gobis, shows, besides sediments and an interbedded lava flow, two inliers, one of the pre-Cambrian limestone, the other of possible Jurassic porphyry flows; both have been brought into view by the stripping away of the sediments rather than by local uplift or by faulting. The later sediments, such as those of Urulji Nuru, doubtless once covered the tops of these inliers and probably even such mountain groups also as the more distant Baga Bogdo, Artsa Bogdo, and the Gurbun Saikhan,—the easterly representatives of the Altai mountain range.

The Oshih beds contain sauropods and primitive armored dinosaur bones and may prove to be Lower Cretaceous (Comanchean) in age.¹ The sediments are entirely of inland continental type—sands, gravels, clays, paper shales, gypsum-bearing clays—and of moist to semiarid climatic association. The entire fauna is non-marine and very difficult to correlate with the faunas of other regions. It clearly represents an inland, relatively isolated basin.² At this remote time, then, Mon-

¹Osborn, Henry Fairfield. 1923. "Two Lower Cretaceous Dinosaurs of Mongolia." *Amer. Mus. Novitates*, No. 95, pp. 1-10.

²Reis, O. 1910. "Die Binnenfauna der Fischschiefer in Transbaikalien." *Explor. Géolog. Chemin de Fer, Sibérie, Petrograd*. Cockerell, T. D. A. 1924. "Fossils in the Ondai Sair Formation, Mongolia." *Amer. Mus. Bull.* (in press).

golia and Angara were dry land, warping into inland basins at first of swampy deposition, with lacustrine and flood-plain types predominating, but later and intermittently developing more pronounced aridity.

ORIGIN OF DEPRESSIONS

In a paper now in preparation, we discuss the origin of depressions in the Gobi desert of to-day, and attempt a review of the literature on this subject. A brief statement must suffice for the present.

The text of this paper will make it clear that the basins cannot all be of the same age; it is very improbable that just the same climates prevailed during all the periods recorded by basin sediments, although we shall offer evidence in another paper to support the thesis that the climate of Mongolia in the past has varied between relatively narrow limits,—between semiarid and desert conditions. It is improbable, furthermore, that the relief was similar in all the periods represented, but it must have ranged from a peneplane to a surface rugged enough to provide coarse rubble. The part played by warping has been touched upon. The basin or depression which now contains the sediments is not by any means coextensive with the original area over which those sediments were deposited, yet we must deal primarily with the basins that have retained sediments to the present day.

We believe that the basins of deposition were not of simple origin, but were the resultant of a number of interacting agencies. To choose a single general case as an illustration, let us suppose, in Tertiary time, a region of moderate relief, including areas of oldrock and of basin sediments, dissected in part by stream work and in part by deflation. The following variable quantities will enter into the problem:—

1. Greater and lesser depth of eroded hollows.
2. Greater and lesser areas of hollows.
3. Hollows or depressions in oldrock areas, where all the sediments deposited in the hollow must be derived from the slow decay of the hard rock. This introduces in turn a new variable, the amount and character of loose material available in the hard rock area. A long quiescent period, and especially a moist climatic rhythm, would have developed a good mantle of soil.
4. Hollows in or near sediment basins, where easily eroded material may be washed out or blown out, offering a great supply of sediment.
5. Disposition, no less than amount, of water supply.
6. Relation of prevailing winds to source of sediments.

Independently of all these variables, it seems necessary to introduce the hypothesis of periodic warping, as will be made clear in the pages that follow.

In figure 6 we show a region of low, mature relief, broad lowlands or hollows alternating with higher regions. In figure 7 these are warped into very gentle swells and depressions, which, save by chance, bear no relation to the topography. Where a downwarp coincides with a lowland, as in figure 7, A-B, the condition will be most favorable to the retention of sediment, and the basin will be filled. Where an upwarp coincides with high ground, as in figure 7, C-D, a broad divide will be formed, from which debris will be washed into surrounding regions. If an erosion-hollow is upwarped, its resultant behavior will depend roughly

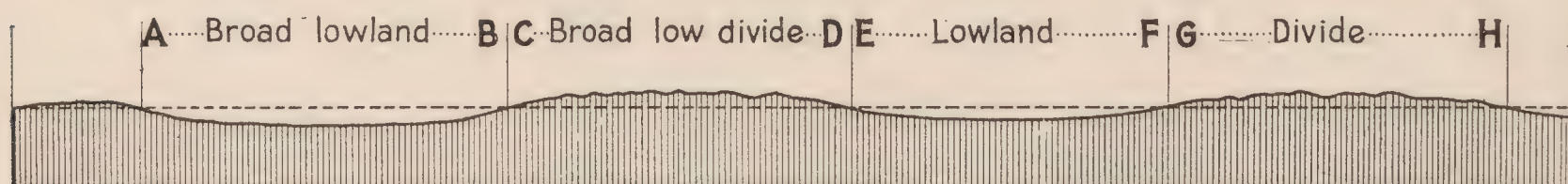


Fig. 6.

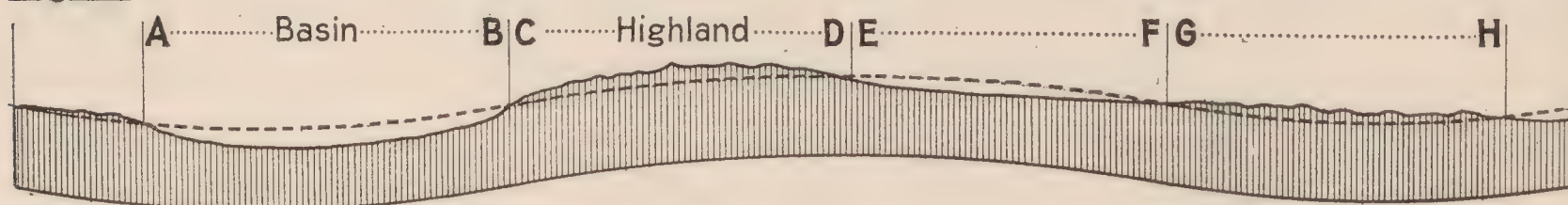


Fig. 7.

Fig. 6. Lay figure of a maturely dissected region of low relief, before warping.

Fig. 7. The same region, after warping,—showing how basins and uplands may be the result of original relief and deformation combined.

Let both higher relief and upward movement be denoted by the + sign, while lowland and downwarp are denoted by the — sign. Then in A-B, both relief and movement are negative, so that a basin is formed. In C-D, both influences are positive, while in E-F and G-H, positive and negative elements combine, making either basin or highland according as the relief factor is greater or less than the warping. Thus in the Oshih basin, Fig. 5, ridges of hard-rock have formed part of the lowland, and have been covered by sediments.

upon the algebraic sum of two opposite influences, the depth of the hollow and the amount of uplift. Thus, if the upwarp is less than the depth of the hollow, as in figure 7, E-F, the hollow still remains, though diminished as a possible repository of sediments. Where a divide is downwarped, it will be included in a basin and will be covered over with sediments, if the downwarping considerably exceeds the height of the divide; otherwise it may still remain a divide.

If we suppose that, in general, the basins formed where all the conditions were most favorable, the amount of warping that need be assumed would be reduced to a minimum. The relative part played by wind and water in the erosion of primary hollows or valleys forms an important subject in itself, and a report on the evidence is in preparation.

TYPES OF GOBI BASINS

Two types of gobi basin are distinguished: first, the faulted or piedmont gobi basin, found along the base of the fault-block mountains of the Altai; and second, the warped or plains type, in the less disturbed areas. The types are not sharply demarked from one another, but the distinctions are instructive.

1. The faulted, or piedmont, gobi basins are distinguished by: (a) greater thickness of sediment; (b) great range in texture of sediment,—including paper shale, fresh-and-brackish-water limestones, clay, sand, gravel and coarse rubble, even with great boulders; (c) wide range of time-periods represented in the sediments,—which implies longer life of the basin as a locus of warping; (d) igneous flows, which are common

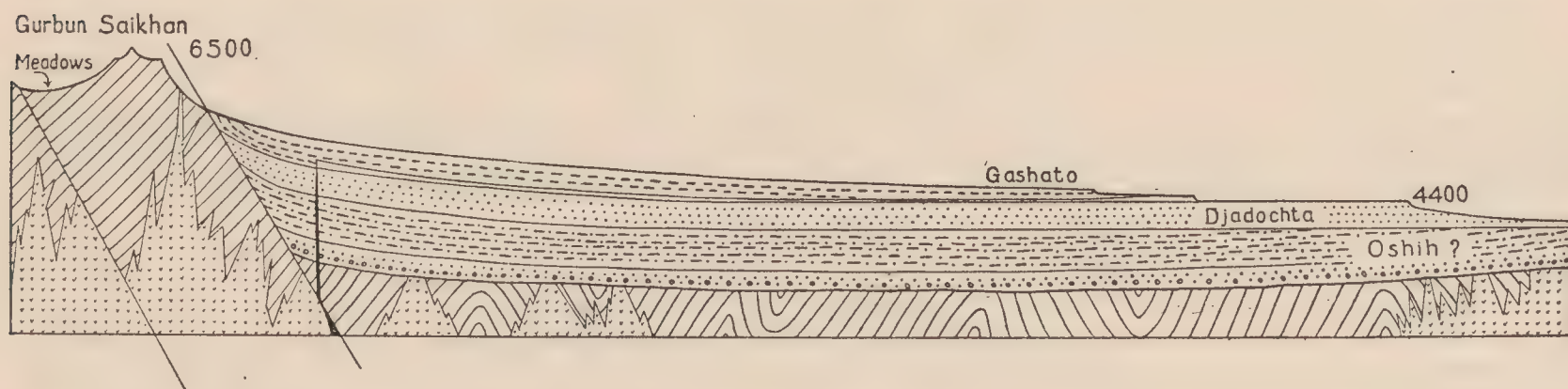


Fig. 8. Cross section of the Djadochta region.

This is a simple faulted type of gobi basin. The beds near the mountain front dip 56° north. Younger beds are encountered as one goes toward the mountain front. In this respect the basin is comparable to the Baga Bogdo piedmont basin, Fig. 10. It is not positively known that Oshih beds underlie the Djadochta; their presence is inferred. Compare with Fig. 11.

in these basins. Volcanism seems to have been associated with faulting, and all the more disturbed basins observed by us contain lava flows (Fig. 8).

2. The warped, or plains, gobi basins are shallower and contain thinner sediments, of but few periods, so that the gaps in the geologic record are even larger than in the sediments of the piedmont basins. The range in coarseness of sediment is less wide—sandy clay, sands and small-pebble gravels predominate. In addition, there are a few occurrences of fresh-water limestones, dense limy marl, marly sandstone, and thin beds of gypsum. None of the warped basins has been markedly disturbed by faulting or tilting.

None of the basins of either type contains a complete record of the sedimentation; none even contains all the horizons represented in Mongolia. In each basin, the sedimentary formations are separated by disconformities or by angular unconformities, representing long gaps or erosion-intervals in the geologic record.

These facts will be considered in some detail, and will be marshaled in support of three theses, as follows:

1. Warping took place in a series of successive increments of movement, separated by pauses or intervals of quiescence long enough in some instances to permit the peneplanation of faulted and warped sediments, and to allow for a complete change of fauna.

2. The locus of warping shifted from place to place; that is, after deposition of one formation in a given basin, warping did not as a rule continue in that basin, but rather in another place, which, in turn, having received a shallow filling of sediment, passed into a quiescent period, and

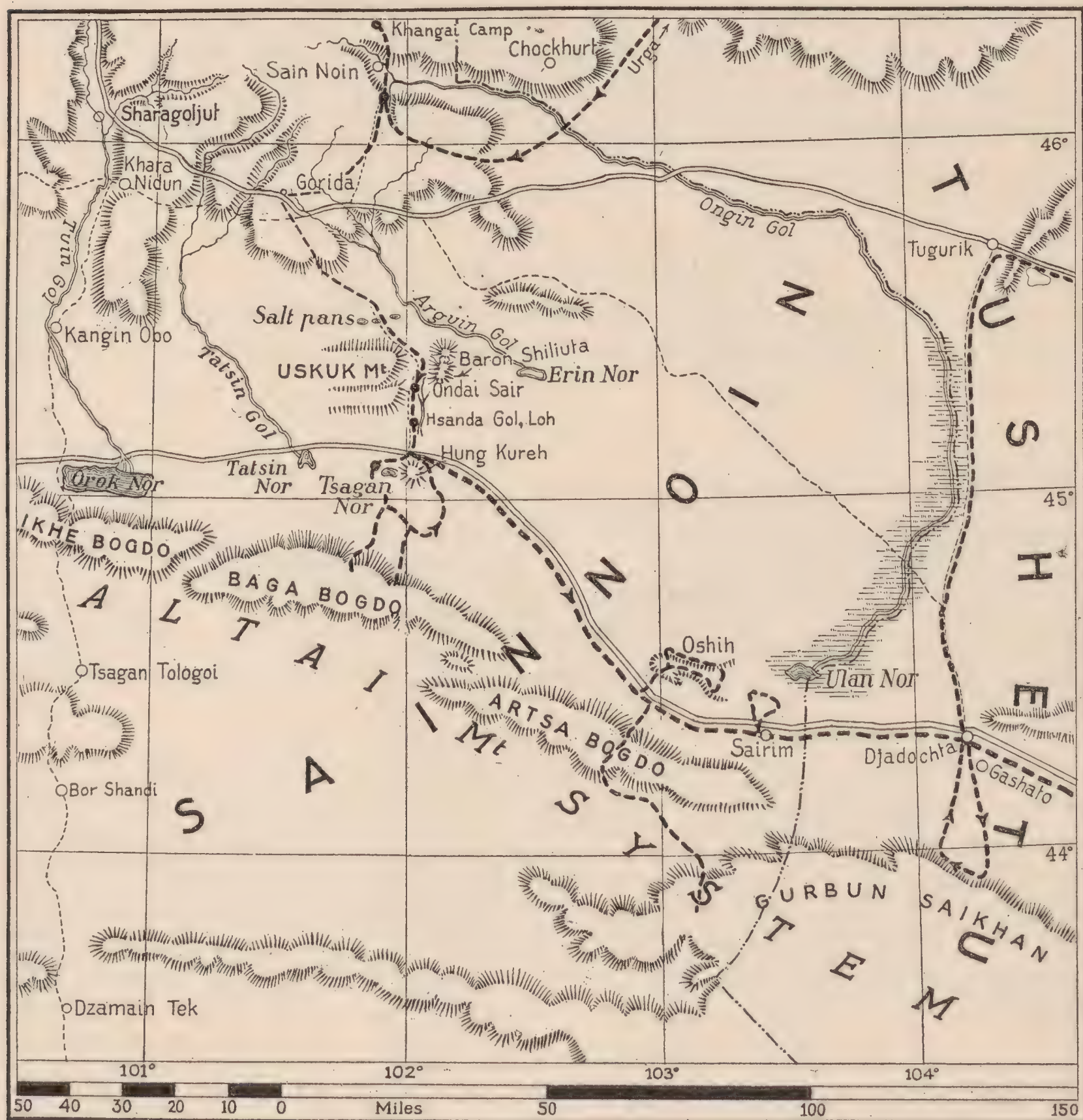


Fig. 9. Sketch map of the eastern Altai region, showing location of stations mentioned in the text.

The limits of the sediment basins are not sufficiently known to justify an attempt to draw them.

the next locus of deposition was in still another basin, or possibly back in the first. Each basin had its rhythm of alternating deposition and quiescence, which probably implied removal of part of the earlier deposit. Some basins, however, continued to warp intermittently during longer periods of time than others.

3. Small units, such as the Mongolian gobi basins, carrying shallow sedimentary fills, probably cannot of themselves set in motion the deep-seated shift of material required by the theory of isostasy. It is not improbable that we sometimes overestimate the effect of the positive weight of the sediments, as well as of the negative load due to stripping of up-arching areas, as the actuating causes of warping. This thesis does not imply that the authors do not accept the principle of isostasy as applying to earth movements of the first magnitude.

We will describe two basins briefly, a faulted or piedmont basin, and a warped or plains basin.

FAULTED OR PIEDMONT TYPE OF GOBI BASIN

Each of three ranges of the eastern Altai, the Baga Bogdo, Artsa Bogdo and Gurbun Saikhan, presents essentially a fault-front along its northern margin (Fig. 9).

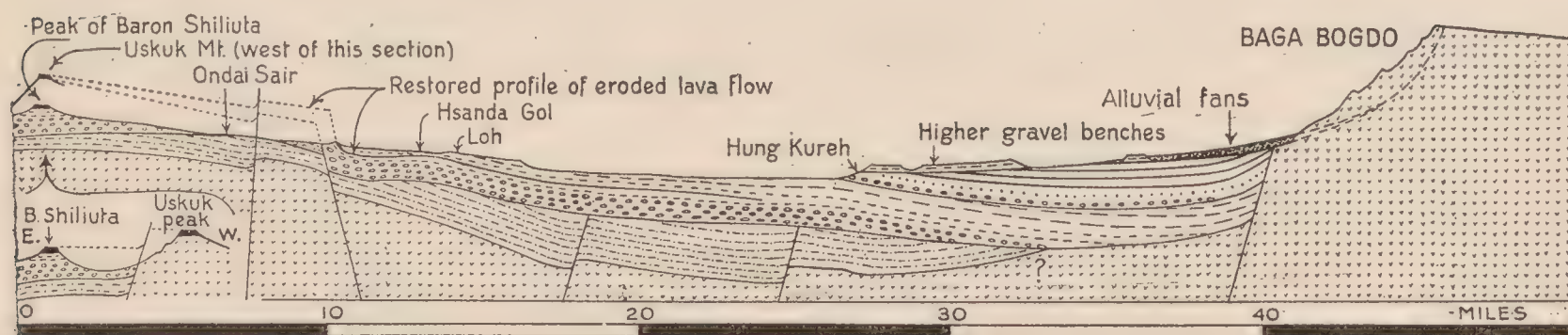


Fig. 10. Cross section of the Baga Bogdo faulted gobi basin.

Though on a much smaller scale, this section is almost continuous with Fig. 4, lying south of the latter. The Uskuk fault-mountain lies just west of the section and so is drawn in dotted lines. Part at least of the sediments once rested upon the Uskuk block, because remnants of sediments have been found upon it, and apparently the same lava flow that is seen in the sediments caps the granite of Uskuk peak. These relations are indicated in the dotted lines. The lava-capped butte, Baron Shiliuta, is seen projected against the higher peak of Uskuk. A short cross section, oriented east-west, is introduced to show the relation between these two peaks. The Cretaceous Ondai Sair beds are much more deformed than the Tertiary formations, which overlie them unconformably. Tertiary beds are also deformed by both faulting and warping. The southern part of the section, between Hung Kureh and Baga Bogdo, is much more disturbed than is represented in this drawing, and carries the latest sediments of the region. The Gobi peneplane is highly developed in this district, and is itself deformed. Since the peneplane bevels Pliocene beds, this section is one of our best means of determining the date of its formation.

In the Baga Bogdo piedmont basin (Fig. 10) the following section is recorded, from oldest to youngest:¹

¹Berkey, Charles P., and Granger, Walter. 1923. "Later Sediments of the Desert Basins of Central Mongolia." Amer. Mus. Novitates, No. 77.

1. The oldrock floor, consisting of schists, marbles, graywackes and slates, all of diverse pre-Cambrian age invaded by granite. Infolded in this complex are conglomerates and sandstones, locally containing seams of coal, which are judged to be Lower Jurassic in age. These form part of the rock floor, not part of the basin sediments.

2. The Ondai Sair sands and paper shales, of Lower Cretaceous (Comanchean) age, resting upon the old floor. They are at least 500 feet thick, and are faulted and tilted.

3. About 3,500 feet of early Tertiary gravels, sands and sandy clays resting unconformably upon the Ondai Sair. They include at least one lava flow, and are in places uptilted and faulted, but they do not share all the disturbances of the Ondai Sair. The higher beds carry the Lower Oligocene *Baluchitherium* fauna, and are called the Hsanda Gol formation, a name which is provisionally extended to the base of the conglomerates, though the lower beds may yet prove to be Eocene.

4. The Lower Miocene clays of Loh, less than 100 feet thick, resting upon the Hsanda Gol clays, without any obvious physical disconformity. Going southward along their dip (Fig. 10), we found that they were succeeded by an undetermined thickness, probably as much as 1,000 feet, of sandy clays and sands, in which as yet no fossils have been found.

5. The Hung Kureh sands and clays, about 2,000 feet thick, gravelly toward the base of the exposure. They carry a fauna of late Pliocene age, according to the opinion of Mr. Walter Granger, paleontologist of the Expedition. They have been disturbed by tilting and faulting, which may be of the same age as that which deformed the older Tertiary beds, but which are probably of later date.

6. A mantle of coarse rubble, clearly derived from Baga Bogdo. This coarse rubble is at least 2,000 feet thick, is partly consolidated, and is unfossiliferous, so far as we now know. Its age may be latest Pliocene or Pleistocene.

The thicknesses of all the formations exposed in the basin add up to 8,500 feet, but, since the whole thickness of some of the members is not known, it may be as much as 10,000 feet. Only a fraction of these strata was accumulated in any one period, yet this basin is the longest-lived and most active basin yet observed in Mongolia, containing the oldest and the youngest basin sediments of which we have record.

Among the features that bear upon the problem of basin-structure may be mentioned the following:

1. The sedimentary formations dip toward the Altai, and younger beds are encountered as we go southward toward the Altai front.

2. The conglomerate at the base of the Tertiary consists of well-rounded pebbles that were derived almost certainly from the Jurassic conglomerate of the general Uskuk region. It would seem that these beds were washed into the basin from the north, rather than from the south, implying that the present Altai was not a notable range in the early Tertiary.

3. The Hung Kureh formation consists of fine materials everywhere except toward the base, where it grades into gravel, and therefore indicates no very marked relief in the Altai region in Pliocene time. The first evidence of rugged relief is the deluge of coarse rubble overlying the Hung Kureh.

We infer from these facts that deformation has been secular and progressive, with long periods of quiescence alternating with periods of disturbance. Thus faulting and tilting took place after the Lower Cretaceous (Comanchean) and after the Pliocene, at least, and possibly after the Miocene as well.

An even more suggestive example is found in the Oshih and Djadochta divisions of the Altai piedmont basin. The Oshih is the piedmont basin of the Artsa Bogdo range. Here are about 2,000 feet of very considerably faulted and tilted sediments. The faults are of small throw, ranging from five feet to 200 feet, and in one instance possibly even more; the dips, apart from drag in the fault zones, do not exceed 24° , and are for the most part 10° or less. The Oshih contains fossils of about the same age as the Ondai Sair and is almost undoubtedly continuous with it.

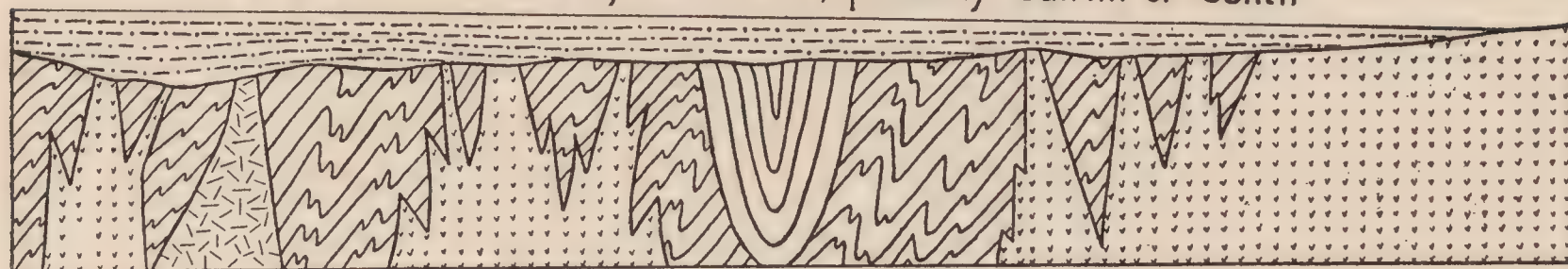
South of the Artsa Bogdo range lies a basin whose sediments contain reptile bones, which Granger judges to be of Oshih age,—indicating either a former extension of the Oshih basin over the site of the present Altai, or an entirely different basin separated from the northern Oshih by a Lower Cretaceous divide.

North of the Gurbun Saikhan, about forty miles east of Oshih, lies a piedmont basin whose floor is not exposed, so far as observed. This basin contains the Djadochta sands, of Cretaceous age, with the *Protoceratops* fauna and the dinosaur eggs. The sand of the Djadochta is very fine, of uniform red color, and about 500 feet thick. The beds dip gently southward into the Gurbun Saikhan piedmont basin, and have been very faintly tilted and arched, but not faulted.

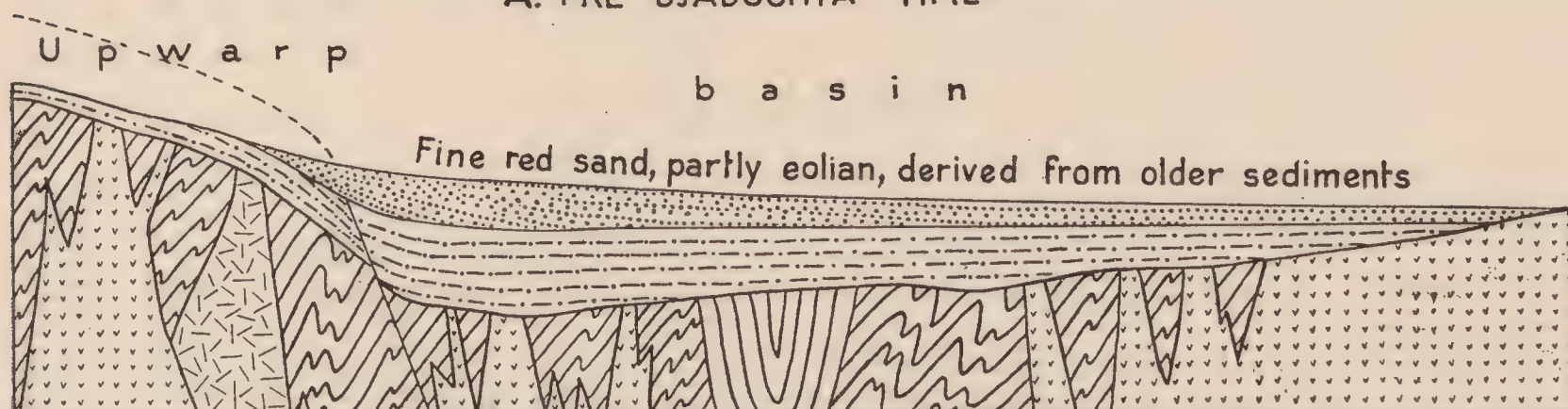
These sands cannot have been derived from the direct weathering of the Gurbun Saikhan, which is composed of such rocks as graywackes, argillites, phyllites, limestones, serpentines and diorites. They must have been derived instead from a preëxisting sand that had already undergone

Site of the Gurbun-Saikhan range

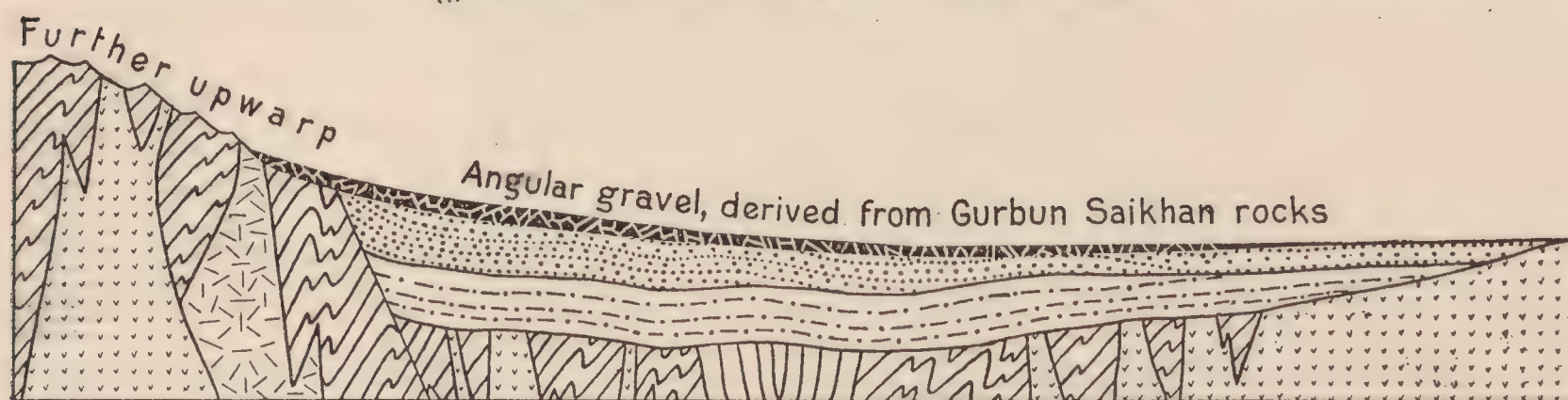
Sandy sediments, possibly Sairim or Oshih



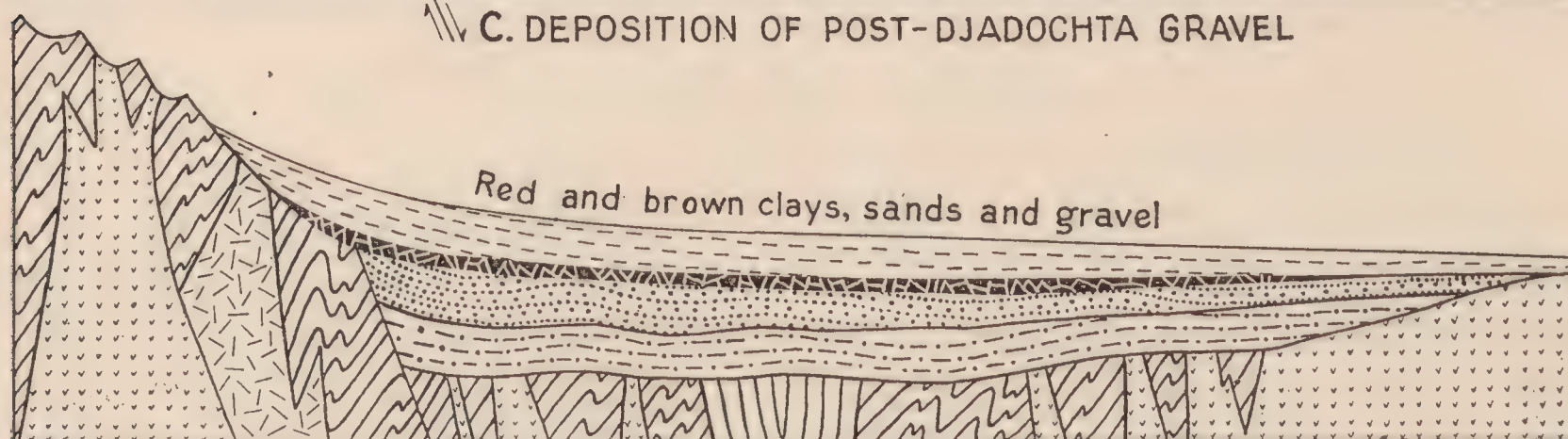
A. PRE-DJADOCHTA TIME



B. DEPOSITION OF DJADOCHTA SANDS



C. DEPOSITION OF POST-DJADOCHTA GRAVEL



D. DEPOSITION OF GASHATO (Paleocene?)

S

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Fig. 11. Four stages of warping indicated in the Djadochta basin.

A shows an old basin of sandy sediments deposited upon a floor of complex old rocks. B shows initial upwarp that caused the Djadochta sands to be washed down into the newly formed basin, without, however, exposing crystalline rocks of the present Gurbun Saikhan range. C shows the deposition of a gravel of angular pebbles, derived from the Gurbun Saikhan rocks, and hence implies that those rocks have been laid bare. D shows the deposition of the Eocene Gashato beds, the peneplaned remnant of which is at least 300 feet thick, and may be much more. The structure of the rock floor of the basin is inferred from the granite exposed to the north of the basin, and the rocks observed in the Gurbun Saikhan range. The successive warpings of relatively small throw suggest the method by which this wing of the Altai was made.

considerable assorting. The only earlier sand of which we have knowledge in the region is the Oshih. Now the highest member of the Oshih that we have seen is a red-and-white sand, called the Sairim member, which is strikingly similar to the Djadochta sand in composition and texture.

Its present easternmost outcrops lie less than forty miles from the present westernmost outcrops of the Djadochta, and both formations must have been more extensive in the late Mesozoic. We suggest that the Oshih, at least in its upper members, may once have overlapped the present site of the Gurbun Saikhan (Fig. 11A). It is not improbable that when uplift began in early Djadochta time, the present Gurbun Saikhan rocks were not exposed, but that the overlying Oshih sands were eroded and washed into the newly formed basin, to become the Djadochta deposits (Fig. 11B). As evidence for this view, we cite the facts that a gravel of angular pebbles overlies the Djadochta, and that these pebbles are all of Gurbun Saikhan origin, which suggests that the next, post-Djadochta, increment of warping brought the Gurbun Saikhan rocks to light (Fig. 11C).

The age of these gravels is known approximately, since they lie underneath the Gashato clays and gravels which carry an early Eocene fauna, according to identifications by Granger (Fig. 11D).

Therefore, the chief dates of warping in this basin fall: (1) in Oshih (Lower Cretaceous) time, when the pre-Djadochta sand-terrane was being deposited over a large part of the eastern Altai region; (2) in Djadochta time (early Cretaceous?); (3) in post-Djadochta time, when the Gurbun Saikhan rocks emerged; (4) in Gashato (early Eocene) time.

WARPED TYPE OF GOBI BASIN

The Irdin Manha basin includes the Iren Dabasu, limited on the north by slate hills, and the Shara Murun, limited on the west by complex old crystalline rocks. The southern boundary consists of hills of granite, schist and graywacke. We have not seen its eastern boundary, but the basin covers an area of at least 10,000 square miles (Fig. 12).

Within the basin is a succession of sediments which do not extend throughout the basin, but which overlap in a complex manner, each occupying a special area (Fig. 13).

The oldest sediment is the Iren Dabasu, of late Cretaceous age, not more than 180 feet thick, resting directly upon the crystallines. It is succeeded by lake beds which, though nearly barren of fossils, yielded a tooth of a small lophiodont, which should prove them Eocene. Upon these barren rocks rest the Lower Oligocene Houldjin gravel, here fifteen feet thick, but apparently thickening northwestward to fifty feet or more.¹

¹Matthew, W. D., and Granger, Walter. 1923. "The Fauna of the Houldjin Gravels." *Amer. Mus. Novitates*, No. 97.

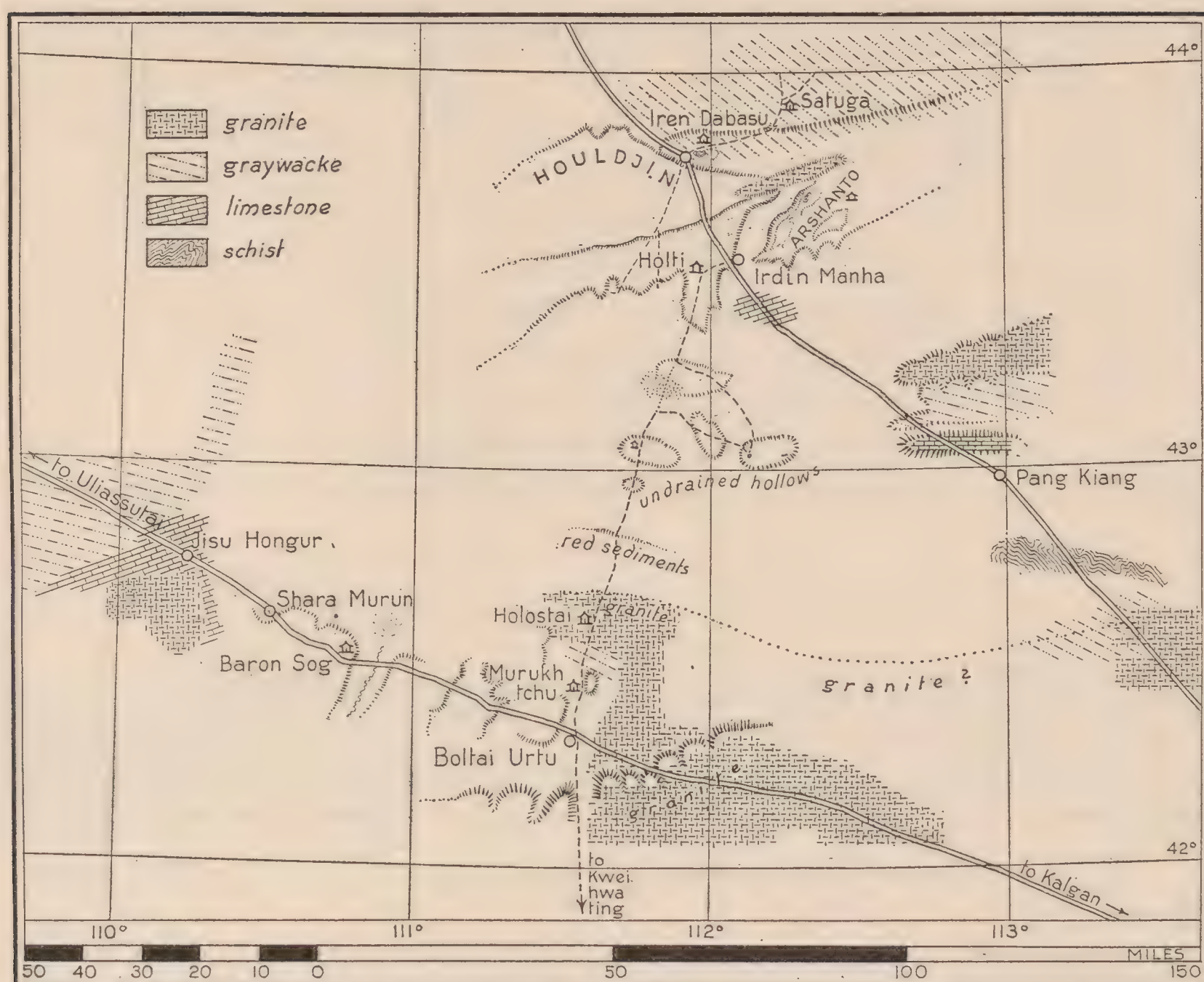


Fig. 12. Sketch map of the Irdin Manha region.

This map serves to locate the stations mentioned in the text, but not to delimit the basin.

At Irdin Manha, twenty miles southeast of Iren Dabasu, the Houldjin is not found, and the section exposed consists of 40 to 100 feet of gray sands, with a rich titanothera fauna, which may be late Middle or even Upper Eocene.¹ Beneath the titanothera beds there are red clays, provisionally called Arshanto, and probably to be correlated with the barren beds above the Iren Dabasu. The Arshanto may prove to be only the lower Irdin Manha, or it may be separated from the Irdin Manha by a disconformity. The base of these beds has not been seen.

The Pang Kiang beds, 60 miles farther south, are about 500 feet thick. In some places at least they rest directly upon the old crystalline rocks. Only one fossil has been found in the Pang Kiang, a fragment of a rodent jaw. Dr. Matthew identifies this as an ochotonid, which is in-

¹Granger, W., and Berkey, C. P. 1922. "Discovery of Cretaceous and older Tertiary strata in Mongolia." Amer. Mus. Novitates, No. 42.

Berkey, C. P., and Granger, W. 1923. "Later Sediments of the Desert Basins of Central Mongolia." Amer. Mus. Novitates, No. 77.

Osborn, H. F. 1923. "Titanotheres and Lophiodonts in Mongolia." Amer. Mus. Novitates, No. 91.

Matthew, W. D., and Granger, W. 1924. "New Carnivora from the Tertiary of Mongolia." Amer. Mus. Novitates, No. 104.

sufficiently diagnostic to serve as an index of the exact age of the formation. He says, however, that this jaw could hardly be older than Miocene.¹ The exact relations of the Pang Kiang to the Irдин Manha must await further field study.

About 75 miles south of Irдин Manha, and 50 miles southwest of Pang Kiang, at the temple Murukh Tchu, a group of clays and sands lies directly upon the crystallines. About 150 feet are exposed, but the thickness may be 200 feet. No fossils were found in these beds.

Twenty-five miles south of Murukh Tchu, at Boltai Urtu, a great mass of conglomerates, about 1,000 feet thick, rests upon the oldrock floor and dips westward and northward away from the oldrock rim of the

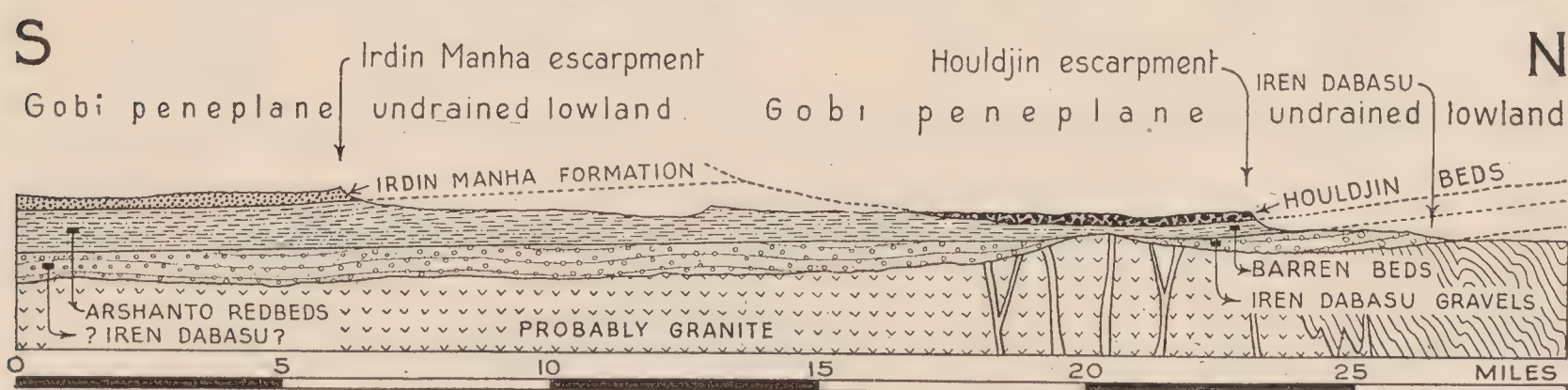


Fig. 13. Cross section of a repeatedly warped basin, from Iren Dabasu to Irдин Manha.

The section shows at least three periods of basin-making, and three unconformities. The unconformities lie (1) at the base of the Cretaceous Iren Dabasu beds, upon the uneven floor of crystalline rocks; (2) at the base of the Middle or Upper Eocene Arshanto (lower Irдин Manha) formation, upon the slightly disturbed Cretaceous beds, and even upon knobs of the old crystallines; (3) at the base of the Lower Oligocene Houldjin gravels, upon the eroded Eocene. Each unconformity implies a long period of quiescence before the deposition of the next succeeding sedimentary formation. The fact that the area became alternately a locus of deposition and of erosion seems to imply a periodic warping of the region. All thicknesses are twice exaggerated.

basin. These conglomerates pass northwestward under and interdigitate with sand and clay sediments which at Shara Murun bear a rich fauna of titanotheres and lophiodonts (Fig. 14). Professor Osborn regards this fauna provisionally as being somewhat younger than the Irдин Manha.²

These complex relations are represented diagrammatically in figure 15. No one place in this broad basin shows a complete section, even of the formations represented in the basin as a whole. All the formations are thin, their combined thickness probably nowhere exceeding 1,000 feet. In most parts of the basin it must fall short of this amount.

There are at least three gaps or breaks in the record, representing non-deposition or even removal of sediment: (1) pre-Cretaceous, a great unconformity, between the Iren Dabasu and the pre-Cambrian slates; (2) Cretaceous-Eocene, between the Iren Dabasu and the "barren

¹Personal communication.

²Personal communication.

beds" (Arshanto?); (3) Eocene-Oligocene, between the barren beds at Iren Dabasu and the Houldjin. Two other disconformities, of very minor value, may possibly be present,—one between the Arshanto and the Irдин Manha, and the other between the Irдин Manha and the Shara Murun.

The basin is not walled in by definite mountain uplifts, nor have we seen evidence to indicate that the hard-rock boundaries are faulted against the basin, except for very minor faulting at the southern boundary, 55 miles south of Iren Dabasu (Fig. 15). It represents, on the contrary, a broad, very gentle warping. The sediments now found in it have less than their former thickness, for the region has been peneplaned.

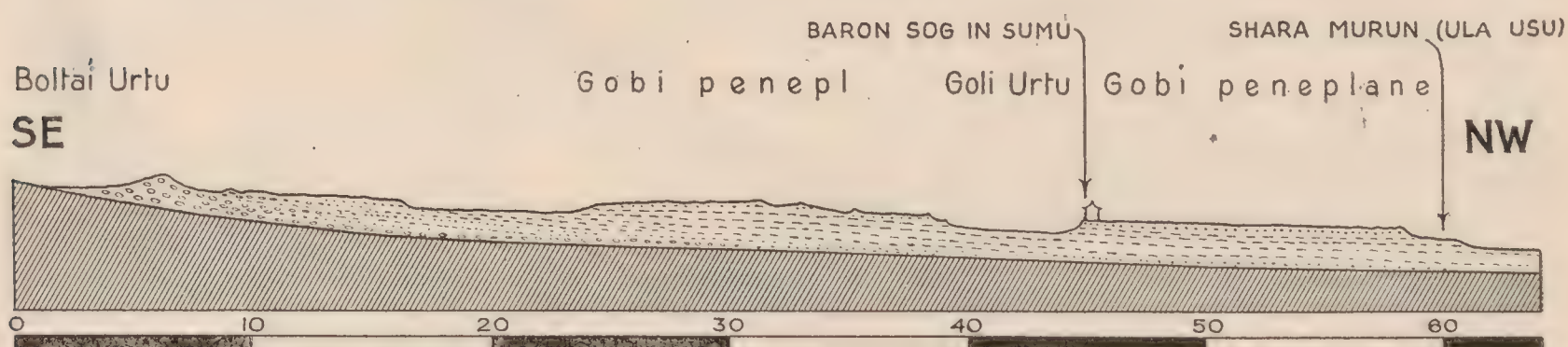


Fig. 14. Cross section of a warped gobi basin, from Boltai Urtu to Shara Murun (see map, Fig. 12).

The section shows conglomerates at Boltai Urtu resting directly upon the complex rock floor. These conglomerates die out westward, passing underneath, and grading into the sands and clays which at Shara Murun carry a rich fauna of Middle or Upper Eocene age.

The relation, too, of the sediments themselves suggests the former greater extent and thickness of the Houldjin at least, if not of the Irдин Manha also (Fig. 13).

The physical history of this great basin must consist of a series of gentle warpings followed by sedimentation, and the epochs of sedimentation were separated by longer periods in which sediments either were not laid down or have since been removed. In the epochs of filling, the deposition exceeded the removal of material from the basin, and this excess of deposition over removal is essentially the measure of warping. In the far longer quiescent periods, removal of material either balanced or exceeded the amount of sediment made available for the streams of that day, so that either no sediments were permanently retained in the region, or, more probably, part of what had been laid down in the preceding epochs of deposition was carried away. The absence of deep channels in the underlying sediments implies that the older beds were reduced to a smooth surface—a local peneplane—before the newer beds were laid down.

The vast lengths of time represented by the periods of quiescence or stability, the thinness of the sediments, the wide area covered and the absence of large faulting or great mountain uplift bordering these basins are all cited to support the thesis that the weight of sediments alone could not have caused the warping; first, because the thickness is too slight to have disturbed the isostatic equilibrium of the earth's crust, second, because the long periods of quiescence indicate that the crust sustained not only the positive weight of the sedimentary load without

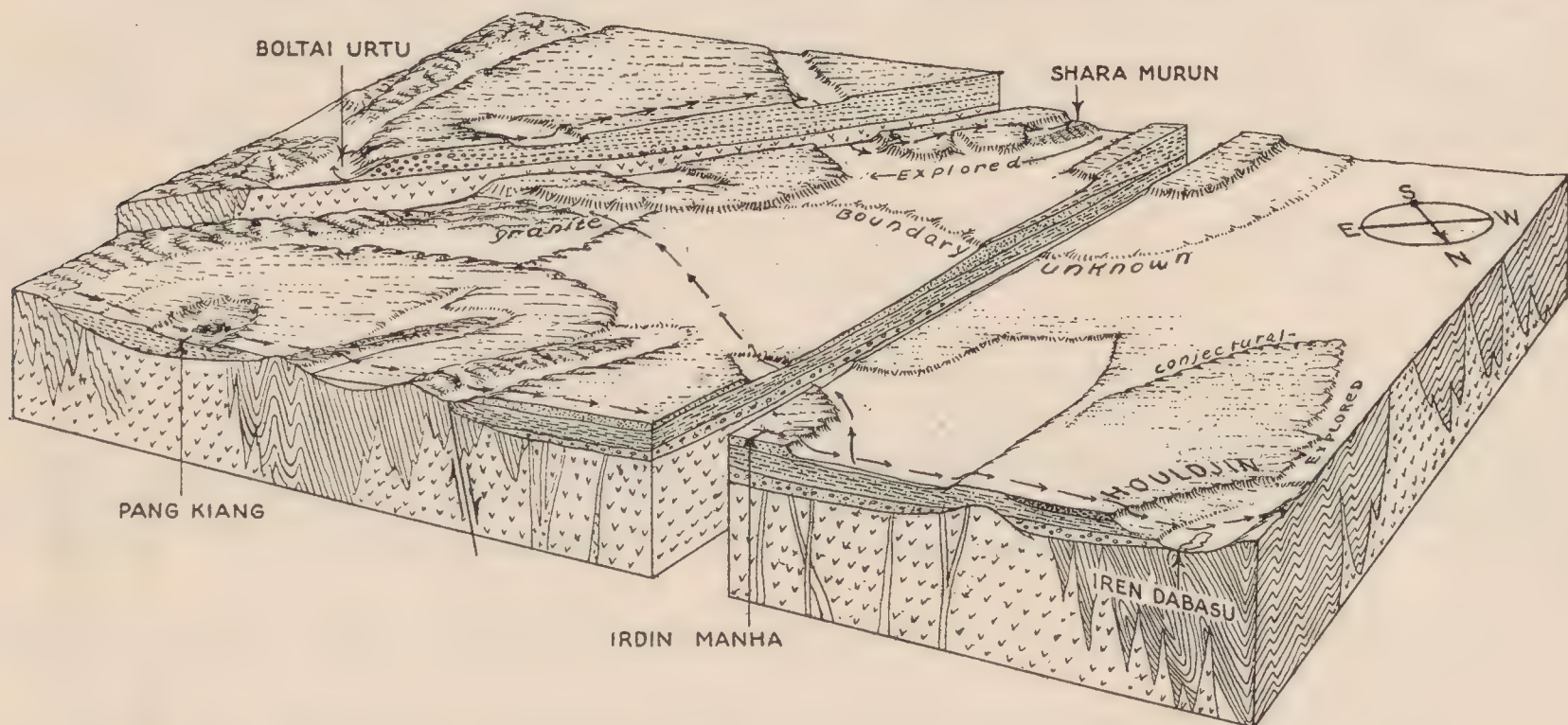


Fig. 15. Block diagram to show the general relations of the formations.

The left-hand or front edge runs northwestward and shows the basins between Pang Kiang and Iren Dabasu (compare with Fig. 13). The rear diagonal cut shows the section between Boltai Urtu and Shara Murun (compare with Fig. 14). The cut from front to rear shows one interpretation of the relations between the Irdin Manha and Shara Murun formations. It is possible that further studies by Osborn, Matthew and Granger may result in correlating these two formations.

being depressed by it, but also the negative load due to peneplanation without being uplifted. Instead, the next deposit of sediment, resting disconformably upon the older deposit, marks a new increment of downwarp following the peneplanation.

GENERAL RELATIONS AND INFERENCES

Many other examples could be offered from every gobi basin we have studied, and all will be described in the larger report now in preparation. But we believe that the examples we have given are typical, and are enough to support the thesis that warping was a slow and discontinuous process, taking place by a series of small increments of movement; and that the sediments are to be correlated with the warping, recording, if the records could be read, both the upwarp that determined the removal of sediment from the upland, and the downwarp of the basin receiving it.

In figure 16 are plotted the thickness of sediments actually observed in the most important basins. Distances and directions between stations are plotted from the westernmost basin at the left to those along the Kalgan-Urga trail at the right. The column for China is generalized from J. G. Andersson's "Essays on the Cenozoic of Northern China."¹

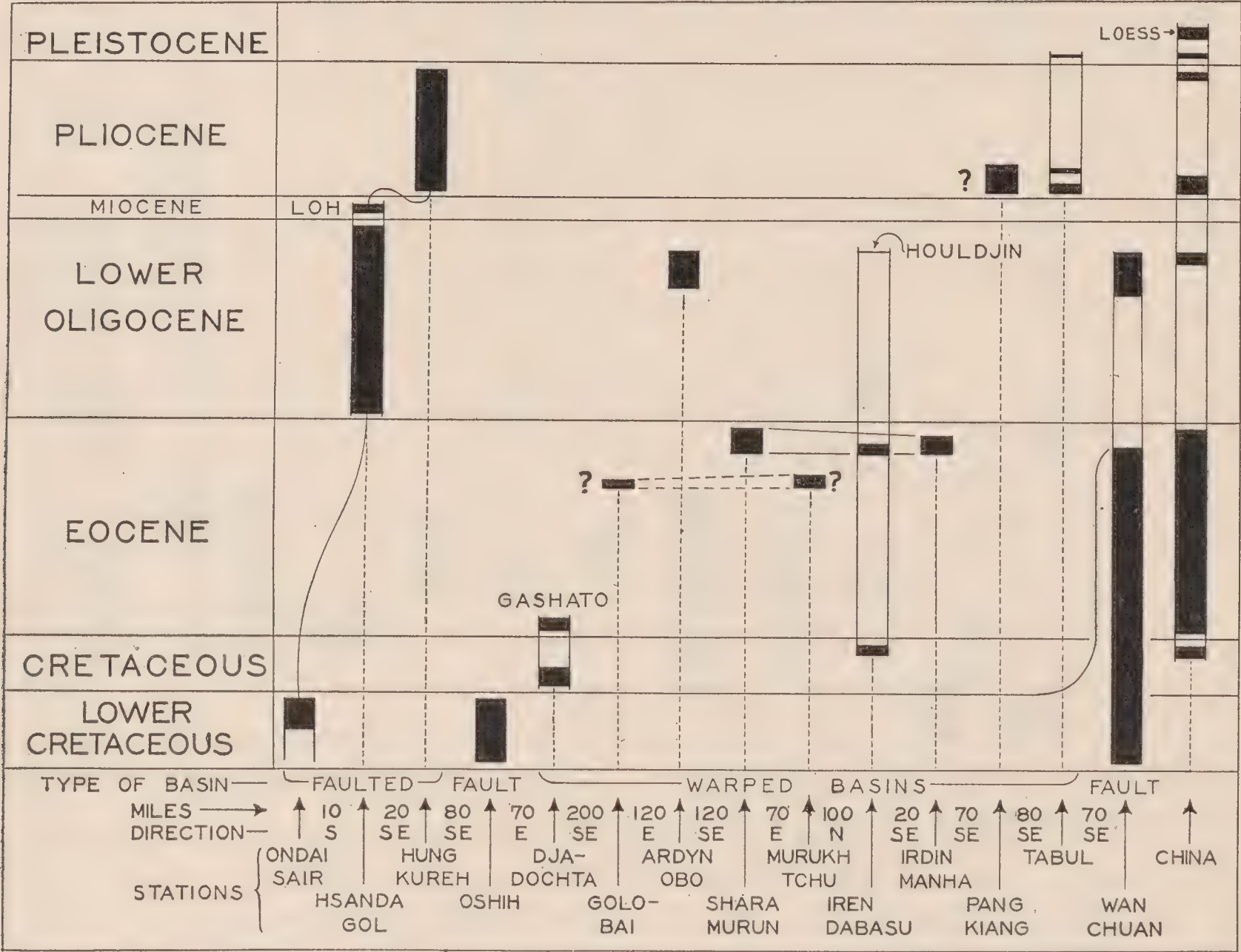


Fig. 16. Columnar diagram of the formations thus far observed in Mongolia.

Thicknesses are plotted to scale. It will be seen that the faulted basins contain far thicker deposits than do the warped basins. The diagram brings out clearly the shifting of the locus of deposition from place to place. The distances indicated at the bottom of the diagram are measured between stations or camps, not between the limits of the basins. The section for northern China is compiled from J. G. Andersson's "Essays on the Cenozoic of Northern China."

The diagram shows clearly the thinness of the sediments actually observed in contrast with the vast lapses of time involved. In figure 17 the columns for Mongolia are condensed into one for comparison as to thickness with those of the Rocky Mountain region, and with the American marine column, emphasizing the relative thinness of the deposits thus far observed in Mongolia.

Among the most interesting inferences which the facts support is the shifting of the locus of deposition from place to place. The Lower

¹1923. Mem. Geol. Surv. China, Ser. A, No. 3.

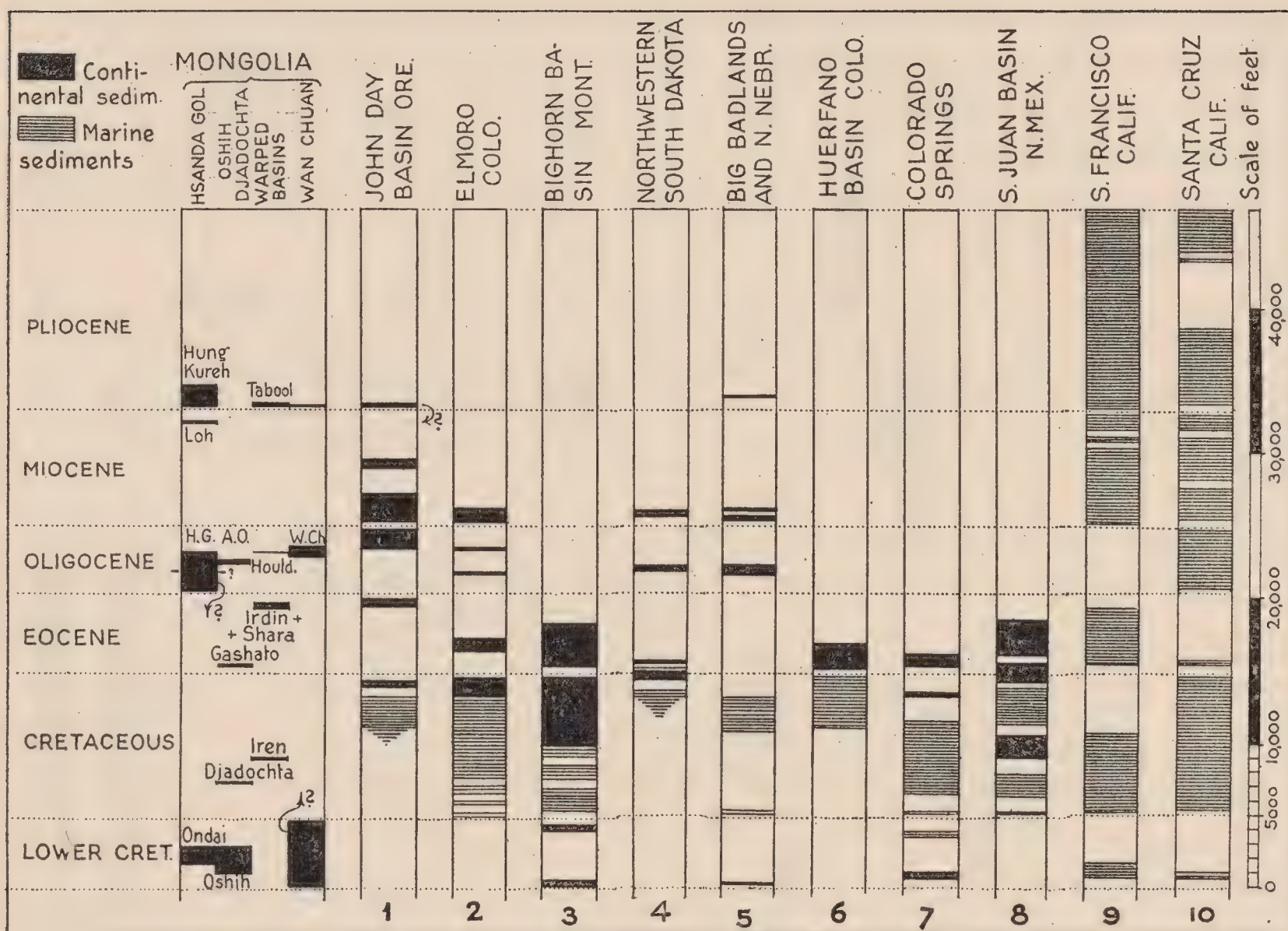


Fig. 17. The columns in Mongolia are shown in condensed form at the extreme left. The numbered columns represent typical sections in the western United States. Formations chiefly of marine origin are represented by parallel lines, while those chiefly of continental origin are in black. References are as follows:

1, Sinclair, W. J. 1909, quoted from Osborn, H. F. 1910. "Age of Mammals," p. 359.—2, Hills, Richard C. 1899. "Elmoro Folio, Colorado," U. S. Geol. Survey, Geol. Atlas, folio 58.—3, Fisher, Cassius A. 1906. "Geology and Water Resources of the Bighorn Basin," U. S. Geol. Survey, Prof. Paper 53.—4, Winchester, Dean E., Hares, C. J., Russell, Lloyd, and Parks, E. M. 1916. "The Lignite Fields of Northwestern South Dakota, U. S. Geol. Survey, Bull. No. 627, p. 16.—5, Darton, N. H. 1905. "Preliminary Report on the Geology and Underground Water Resources of the Central Great Plains," U. S. Geol. Survey, Prof. Paper 32. Wanless, Harold R. 1923. "The Stratigraphy of the White River Beds of South Dakota," Proc. Am. Phil. Soc., LXII, No. 4.—6, Osborn, H. F. 1897. "The Huerfano Lake Basin, Southern Colorado, and its Wind River and Bridger Fauna," Bull. Am. Mus. Nat. Hist., IX, Art. 21.—7, Finley, George I. 1916. "Colorado Springs Folio, Colorado," U. S. Geol. Survey, Geol. Atlas, folio 203.—8, Sinclair, W. J., and Granger, Walter. 1914. "Paleocene Deposits of the San Juan Basin, New Mexico," Bull. Am. Mus. Nat. Hist., XXXIII, Art. 22. Bauer, C. M., and Reeside, J. B., Jr. 1920. "Coal in the middle and eastern parts of San Juan County, N. Mex.," U. S. Geol. Survey, Bull. No. 716 (g).—9, Lawson, Andrew C. 1914. "San Francisco Folio, California," U. S. Geol. Survey, Geol. Atlas, folio 193.—10, Branner, J. C., Newsom, J. F., and Arnold, Ralph. 1909. "Santa Cruz Folio, California," U. S. Geol. Survey Geol. Atlas, folio 163.

Cretaceous Oshih and Ondai Sair gobi basins are almost certainly connected. Deposition must have begun in the Oshih earlier than in the Ondai Sair, since the Oshih beds are thicker, coarser and carry a fauna of rather more primitive aspect, and since the paper shales and large sauropods are found only in the upper beds of the Oshih, whereas they occur in the lower beds of the Ondai Sair. After deposition of the Oshih and Ondai Sair, sedimentation in this region ceased, or, if beds were deposited, they have been removed by erosion; but at Djadochta, forty miles east of Oshih, a gobi basin received 500 feet of early Cretaceous fine red sands probably derived from the destruction of Oshih beds. The next Mesozoic deposits of which we have knowledge are at Iren Dabasu, 380 miles farther east, where late Cretaceous beds rest directly upon pre-Cambrian slates. The locus of deposition had shifted, therefore, during Lower Cretaceous (Comanchean) and Cretaceous time.

Returning to the Altai and referring again to figure 16, the Gashato beds, which are the lowest Eocene strata we have seen, rest on the angular gravel which covers the Djadochta red sands (Fig. 11). The gap between the Djadochta and the Gashato represents the time recorded in the Iren Dabasu trachodont beds, plus an interval of Cretaceous and Paleocene or Eocene time that has left no sedimentary record so far as we now know. No younger formation was seen in this region, but both to the west and to the east there are later sediments. The Irдин Manha and the Shara Murun formations represent the highest Eocene yet found in Mongolia. They rest in some places upon the oldrock floor, but in other places they may lie upon Cretaceous or older Eocene sediments.

Thus, although we do not know the age of the Murukh Tchu or the Golobai, the facts demonstrate that there has been a shifting of the locus of deposition during the Eocene from the Altai region in earlier Eocene toward the Iren Tala in later Eocene time.

The oldest Oligocene beds yet seen in Mongolia are, apparently, those of Ardyn Obo, which rest directly upon the crystalline oldrock floor. The Oligocene of the Houldjin bench at Iren Dabasu should be rather younger, since it contains *Baluchitherium* bones. The *Baluchitherium* beds of Hsanda Gol have been called Lower Oligocene by Dr. Matthew.

Whether or not these three formations prove to be of the same age, the evidence of shifting of the locus of deposition is convincing. In at least three widely separated regions, warping recommenced in Lower Oligocene time, so that beds of this age were laid down, in one locality upon eroded Lower Cretaceous (Comanchean) beds, in the second upon

the bare crystalline rocks, and in the third upon Eocene beds of doubtful correlation, somewhat older than the typical Irдин Manha (Fig. 16).

The only Miocene beds yet seen in Mongolia are those of Loh, which rest upon the Hsanda Gol without any notable appearance of a break in sedimentation. Thus far, this is similar to the findings in China where Dr. Andersson¹ refers a few beds to the "Lower Pliocene or Upper Miocene."²

This almost complete absence of the Miocene over vast areas of basin-lands constitutes one of the major problems of the region. Some of the elements of the problems are:

1. No marine Miocene beds are known in northern Asia, though Miocene lignites are reported as far north as the New Siberian Islands³ hence the sea was remote and the Angara-Gobia continent was broad during that period.

2. The suggestion made by the patchy distribution of the earlier formations, as already recited in this paper, is that the deposits are all inland deposits. Despite the intermittent warping to form basins and receive sediments, therefore, the continent as a whole was stable and was undergoing removal rather than deposition of sediments.

This should imply either that we should find inland sediments of Miocene age more extensive than we have yet found, or that northern Asia was undergoing marked erosion during the Miocene.

The gaps in the record may represent periods of relative quiescence in which sediment was not being deposited, or was being eroded. If an upwarp was in progress, it is hard to see why a corresponding deposition should not be found as a record of it, unless the entire region was subject to erosion at the time. Such general erosion would be recorded in a peneplane, like that which beveled the Mesozoic beds prior to the deposition of the Tertiary. The preservation of vast areas of relatively thin, soft sediments, which represent many diverse horizons, and which are slightly or not at all disturbed, leads one to believe that the country was not greatly uplifted, and that it was suffering but little warping or denudation during the long intervals represented by the gaps in the sedimentary record.

¹Andersson, J. G. 1923. "Essays on the Cenozoic of Northern China," Table II. Mem. Geol. Surv. China, Ser. A, No. 3.

²A note recently published, entitled "Biological and Palaeontological Collecting in Northern China," in the China Journal of Science and Arts, II, 1924, pp. 72-73, states, "The most recent expedition carried out by the two scientists [referring to Père Emile Licent and Père Teilhard de Chardin] resulted in the discovery in the valley of Shara Ossa Gol, a river in Mongolia to the north of Kansu, of a rich find of fossils and archaeological specimens in deposits running in a complete series from the Miocene of the Upper Tertiary to recent strata of Neolithic age."

³Toll, Baron E. W. 1900. "Carte géologique du Nord de la Sibirie Orientale," reproduced in Petermann's geographische Mitteilungen, XLVI, Pl. XIII, quoted from Suess, 1902. "La Face de la Terre." III, 1, p. 29.

It seems to follow, independently of the inferences just offered, that the weight of the sediment could have had no causal relation to the depression of the earth's crust. The fact that areas as large as 10,000 square miles in extent are floored by thin formations, as in the case of the Irdin Manha-Shara Murun basin, seems to indicate that these beds were laid down upon a relatively flat surface that did not tend to sink under the load. The crust evidently supported these and other formations while they were peneplaned. The peneplanations are taken to imply great stability and rigidity of the bedrock floor,—that is, the crust neither sank under the load sufficiently to deform the sediments and encourage thicker deposits, nor rose under the negative load, when the region was eroded to a peneplane. In a paper to be offered later, a review of the diastrophic periods in Mongolia will be attempted, but at present it is enough to say that we believe that isostatic balance can be upset only by very large positive and negative loads, and that the stripping and loading observed in Mongolia have been of an order of magnitude too small to overcome the inertia of the earth's crust, even where fault lines exist. In the dynamics of the region, the sediments played a passive part. Basin-warping and mountain-building were complementary parts of a great orogenic movement or succession of movements, and were controlled, we believe, by deep-seated causes.



Fig. 1. Map of the Gobi region.

The mountainous areas are shaded with slanting lines; the lowlands are white; the deeper depressions are stippled.

Ondai Sair is indicated by the index letters OS, south of the letters MTS of KHANGAI MTS. Ust Balei is not marked on the map, but it lies on the large river that leads northwestward out of Lake Baikal, near the prong of mountain-country that projects toward this river from the Sayan ranges.

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Article VI.—FOSSILS IN THE ONDAI SAIR FORMATION, MONGOLIA¹

BY T. D. A. COCKERELL

INTRODUCTION

I am indebted to The American Museum of Natural History for the opportunity to study a most interesting collection of fossils in the paper shales of the Ondai Sair formation of the Gobi Desert. These were collected by Messrs. Charles P. Berkey and F. K. Morris, on the Third Asiatic Expedition of the Museum. Messrs. Berkey and Granger (American Museum Novitates, No. 77) discuss the Ondai Sair formation, and state that it is "at least as old as the Cretaceous, perhaps the Lower Cretaceous or Comanchean, rather than the Upper Cretaceous. In this locality, at Mt. Uskuk, the series is sharply delimited by an unconformity, above which no fossils of this type are to be found; and it is limited also below by a much greater unconformity, beneath which lie folded strata with coal beds, conglomerates and intrusives, all judged to be of Jurassic age, as well as many still older formations."

¹Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 37.

Mr. Frederick K. Morris has been good enough to write me at considerable length, summarizing the observations and conclusions of the investigators. I venture to quote the following:

“We found the fish-bearing paper shales associated with sandstones in which were sauropod reptiles at Ondai Sair. At the Oshih (Ashile) basin we searched the paper shales this year again for fossils, but found only the remains of a few plants, too badly macerated prior to deposition to be identified. The paper shales of the Oshih basin carry gypsum crystals, which perhaps points to bitter waters in which the fauna of Ondai Sair could not live. The Oshih and Ondai Sair basins are very probably continuous and form one basin. Sauropods and primitive predentates are found in each locality, although perhaps there is a slight difference between the two faunas. At Oshih the paper shales lie far higher in the series, not less than five hundred feet above the chief sauropod beds; but a few large sauropod vertebræ were seen only one hundred feet below a horizon which, on other grounds, we believe is correlated with the paper shales. At Ondai Sair, as I have said, the sauropods are found close to the paper shales and essentially of the same age.

“Fish-bearing shales are found in North China and have been called Jurassic, on the assumption that the fishes were indeed the *Lycoptera middendorffi* described by Reis. Paper shales were seen by us on the main road to Urga, between Ude and Tuerin, but our brief search of them did not reveal any fossils. We think this basin may be of the same age as the fish shales of Ondai Sair.

“The Oshih-Ondai Sair basin is the oldest true basin found by us in Mongolia; its sandstones rest directly upon the strongly disturbed old rocks that have passed through one or more mountain-bearing revolutions. At Ondai Sair the basement was chiefly pre-Cambrian rocks—graywackes and slates invaded by granites. At Oshih less is seen of the basement, but we found an inlier of crystalline limestone, cut by syenite and granite; also other inliers of the old graywacke series of which the Altai range to the south is principally composed; and a younger chain of strongly folded porphyries, which may be what Doctor Berkey and I judged to be Jurassic in other localities last year. Clearly, there is a great unconformity beneath the Oshih and Ondai Sair and, so far as we know, these basins, which carry the paper shales, date the beginning of the basin or gobi sedimentation; that is, the beginning of deposition of shallow masses of continental sediments—alluvial fans, flood-plains, deltas, playa lake deposits and, locally, deposits in shallow but more permanent lakes. These deposits are but little disturbed and it is in them that all the vertebrate fossils are found.

“The accurate dating of the oldest of these basin deposits is of great importance, not only for paleontology but for the dating of the last great disturbance prior to the Altai uplift.

“We found marine beds of Permian age involved in the older mountain-folding. Apparently younger than these, is a vast series of shales, sandstones, conglomerates and surface volcanic rocks—ash, tuffs and flows of rhyolite, trachyte and basalt which are strongly folded. After folding, these rocks had been eroded to a peneplane. This latter series is wholly non-marine and carries obscure plant remains and, locally, coal. We named these rocks the Tsetsenwan series.

“South of Mongolia the Lower Jurassic in northern China carries coal and is strongly folded, even slaty in places, and has porphyries very like those in the Mongolian series just mentioned. In northern China, therefore, a folding took place sometime between Middle Jurassic and late Jurassic time. In view of the physical similarity between the Lower Jurassic rocks of the Western Hills and the Tsetsenwan series in Mongolia, and because in China also the fish-bearing shales are not severely disturbed, it has seemed to us that for reasons of structural geology it is likely that the earliest basin lands are possibly of Comanchean age. The “Upper Jurassic or Lower Cretaceous” of Reis may well be what we call in America, Comanchean.

“The significance of the Ondai Sair fauna is increased when we consider that there is apparently a chain of basins extending from Siberia across Mongolia into China; if the fauna proves to be the same or of nearly the same age in all, this fact would correlate the entire column of post-mountain-folding, continental sediments in the three regions.”

ONDAI SAIR BIOTA

The following species were obtained by the Expedition in the Ondai Sair formation:

Reptilia: *Protiguanodon mongoliense* Osborn, Amer. Mus. Novitates, No. 95, 1923.

Pisces: *Lycoptera middendorffi* Johannes Müller, 1848. Exceedingly abundant in the paper shales (Pl. II, fig. 1). The specimens agree with *L. middendorffi* in the proportions of the fins, rather than with *L. sinensis* A. S. Woodward, from the Lower Jurassic (?) of the Province of Shantung, China. These fishes will be discussed more fully in a later contribution; they form a new family, **Lycopteridæ**, apparently

ancestral to the Cyprinidæ, and have scales scarcely differing from those of the European minnow.

Crustacea: *Estheria middendorffi* T. R. Jones, 1862. Exceedingly abundant in the paper shales (Pl. II, fig. 2).

Insecta: *Ephemeropsis trisetalis* Eichwald, 1864
Ephemeropsis melanurus, new species
Cymatophlebia (?) *mongolica*, new species
Trichopterella torta, new species
Indusia reisi, new species
Chironomopsis gobiensis, new species
Coleoptera, spp. incert.

Plants: *Baiera furcata* (Lindley and Hutton)
Phyllocladites (?) *morrisi*, new species
Czekanowskia sp.
Equisetaceæ (?) fragments

Concerning this biota, we have to ask, (a) does it appear, taken as it stands, to be Upper Jurassic or Lower Cretaceous? (b) is it identical, or nearly identical, with that of the supposed Upper Jurassic fish shales of the Transbaikal country directly north of the Gobi Desert?

With regard to the first question:

(1) The dinosaur, I learn from Dr. W. D. Matthew, is provisionally referred to the Cretaceous, but it is not of itself decisive as to age.

(2) The fish is singularly modern in aspect and affinities, but it belongs to a type always considered Jurassic.

(3) The *Estheria*, as an organism, is of no value in determining age, except within very wide limits. Similar species are living today.

(4) The insects do not clearly indicate age; they are on the whole of modern type, but such forms are known to occur in the Jurassic.

(5) The plants appear to represent a Jurassic flora, but similar forms have been found in the Cretaceous. Thus the contemplation of this biota apparently leaves us where we were before, in uncertainty as to whether it is Upper Jurassic or Lower Cretaceous.

Turning now to the second question, it must evidently be answered in the affirmative. The Transbaikal fish shales are found in several places, for instance: Turga, about 60 miles north of Mongolia, directly north of the Gobi Desert; Konduevskoe or Konduyewskaya, about 90 miles due east of Turga; Nertchinsk or Nertstschinsk, 100 miles north-northwest of Turga.

These shales are, just as those from Ondai Sair, full of *Lycoptera middendorffi*, *Estheria middendorffi* and *Ephemeropsis trisetalis*; they also

carry plants which appear to be *Baiera* and *Czekanowskia*. It does not appear possible that such an association could occur in two deposits of very different age. I have not had access to the important paper by O. Reis, "Die Binnenfauna der Fische in Transbaikalien," Explor. Géolog. chem. de fer Sibérie (Petrograd, 1910), but Mr. Morris has sent me photographs of the plates, with explanations, and a brief statement of Reis's position. The beds have always been considered Upper Jurassic but Reis confessed to finding in the fauna puzzling affinities ranging from early Tertiary to Jurassic, although the strongest bonds appeared to be with the Upper Jurassic or Lower Cretaceous.

As Reis records a number of organisms not yet found in the Ondai Sair, it will be well to review the more significant of them:

(1) Some additional fish remains are too fragmentary to be of much value. One of these, based on some fins, is called *Stichopterus woodwardi*. The generic name is new and has been omitted from Jordan's Classification of Fishes and Genera of Fishes. The genus is, however, probably unrecognizable.

(2) There is a series of Mollusca, referred to *Lymnæa*, *Paludina*, *Cerithium* and *Cyrena*. *Lymnæa obrutschewi* Reis is closely similar to *L. accelerata* White, from the Comanchean near Cañon City, Colorado, except that it is smaller. *Paludina pura* Eichwald very closely resembles *Lioplacodes veternus* Meek and Hayden, from the American Jurassic, but is also smaller. It is a shell with much the aspect of the modern *Bythinia tentaculata* Linné, but I think it is safe to call it *Lioplacodes purus*.¹ *Cyrena pusilla*² Reis is a very small species but characteristic of the genus and having the general form of Cretaceous species. *Cerithium gerassimowi* Reis is not closely related to anything known to me, but the approximately similar types belong to later epochs.

(3) The additional insects are of no consequence. One beetle is named *Carabites latecostatus*, but its family position is uncertain.

(4) Numerous ostracods are recorded by Joseph Georg Egger, with a plate of figures. They are referred to described species, but distinctive characters are few and I do not know what reliance can be placed on them. Our confidence in the determinations is not increased by finding one of the species referred to *Cypris faba*, the common ostracod of the Miocene at Wangen (Eningen) in Baden.

(5) The additional fragmentary plants convey little information. *Pinus witimi*, based on a winged seed, suggests a much later epoch; but

¹Comparison may also be made with the genus *Baikalia* Martens, living today in Lake Baikal.

²The name *Cyrena pusilla* is preoccupied by *Cyrena pusilla* "Parreyss," Phil., Abbild. II. 78. *Cyrena*, Tab. 1, f. 7 (February 1846), from the Nile. The fossil species described by Reis may be known as *C. reisi*, new name.

there is no reason why this should not be called *Pityospermum witimi*. The genus *Pityospermum* of Nathorst includes winged seeds resembling *Pinus*, found in the Jurassic. Another Siberian species, *Pityospermum maackianum*, was described by Heer as *Pinus maackiana*.¹

UST BALEI BIOTA

There remains one other method of attacking our problem, by comparison with the biota of the Ust Balei beds, north of Irkutsk and west of Lake Baikal. These beds were first mentioned by Trautschold in 1867, and since then have proved fruitful of plants and insects. They are universally recognized as Jurassic and generally ascribed to the Middle or "Brown Jura," more or less equivalent to the Lower Oölite. Since those who consider the *Lycoptera* shales Jurassic, agree in placing them in the Upper Jurassic, it is not to be expected that they should carry the same biota as the Ust Balei; but there might be some similarity.

The Ust Balei insects, as recorded, number about 25 species, as follows:

- Blattoidea: *Ophismoblatta sibirica* (B., R. and G.)²; *O. maculata* (B., R. and G.). The first is a wing, the second a nymph.
- Mantoidea: *Pseudohumbertiella grandis* (B., R. and G.). Based on half a wing; was supposed to be a mantid, but Handlirsch thinks it may better be referred to the locustoids.
- Dermaptera: *Baseopsis* (?) *sibirica* B., R. and G. Based on the anterior half of an insect; was supposed to be an earwig, but Handlirsch regards it as unrecognizable, perhaps a beetle larva.
- Orthoptera: *Parapleurites gracilis* B., R. and G. A good tegmen, referred by Handlirsch to his family Locustopsidæ.
- Panorpatae: *Mesopanorpa hartungi* (B., R. and G.). Referred to the family Orthophlebidæ.
- Plecoptera: *Mesonemura maacki* B., R. and G. (imago); *Mesoleuctra gracilis* B., R. and G. (larva); *Platyperla platypoda* B., R. and G. (larva).
- Ephemeroidea: *Mesobaëtis sibirica* B. R. and G.; *Mesoneta antiqua* B., R. and G. These are May-fly nymphs of

¹This is spelled *maakiana* in the books, but it was named after Maack, the celebrated Siberian explorer.

²Brauer, Redtenbacher and Ganglbauer (1889).

ordinary size, quite unlike the giant forms of the fish shales.

Odonata: *Palæophlebia synlestoides* B., R. and G. (an imperfect wing). *Samarura gigantea*, *minor*, *pulla*, *angustata* and *rotundata*, all of B., R. and G. (nymphs).

Coleoptera: *Carabocera prisca* B., R. and G.; *Timarchopsis czekanowskii* B., R. and G.; *Doggeria sibirica* Handl.; *Memptus braueri* Handl.; *M. redtenbacheri* Handl. Five beetles of rather doubtful affinities. *Elaterites sibiricus* Heer is said to come from Irkutsk.

Diptera: *Mesopsychoda dasyptera* B., R. and G.

Lepidoptera or Homoptera: *Phragmataecites damesi* Oppenheim; *Palæocossus jurassicus* Oppenheim; two remarkable insects considered by Handlirsch to be primitive Lepidoptera, but Tillyard has recently given apparently conclusive reasons for referring the Palæontinidæ to the Homoptera. They are recorded from East Siberia, and were, I presume, from Ust Balei.

These insects show no affinity with those of the fish shales, and since they constitute an analogous fresh-water and lake-side fauna, the absence of the large ephemerids is especially noteworthy. The number of species (especially in view of the fragmentary condition of many) is too small to permit any very decisive conclusions, and it is much to be desired that the locality should be explored again for additional material. We can, however, state that the Ust Balei fauna is not that of the fish shales.

Heer described a number of plants from Ust Balei, but as Seward has shown, his work needs radical revision. So far as we know it, the flora does not seem to correspond with that of the fish shales.

We must then conclude that the fish shales of Ondai Sair and the Transbaikal contain a fairly homogeneous biota, which must be approximately of one age. This biota is quite distinct from that of the Ust Balei beds, and presumably much later. It may be Upper Jurassic, but there is no proof that it is not Lower Cretaceous. Actually, it presumably belongs to a period near the beginning of the Lower Cretaceous and its classification as Jurassic or Cretaceous may be merely a matter of arbitrary definition. In any event, this biota, which represents an early stage in

the development of a number of groups still surviving, is of great interest and well merits further investigation.

INSECTS

EPHEMERIDA

(PLECTOPTERA)

The May flies were well developed as early as the Permian, with many genera. Numerous species are known from the lithographic stone of Bavaria (Jurassic), and a series of nymphs or larvæ has been obtained from the Jurassic rocks of Siberia. The Permian species, constituting a family, Protereismatidæ, are remarkable for having the hind wings as large, or nearly as large, as the upper. Nevertheless the venation is singularly modern, as can be seen by comparing the Permian *Prodromites*¹ *rectus* (Sellards) with such a genus as the living *Ameletus*. Thus it may be said that at least some of the Permian wings approach the modern Siphonuridæ in structure and it is therefore perhaps less surprising to find apparently genuine siphonurids in the Jurassic. The genus *Pædephemera* of Handlirsch, with four species in the lithographic stone of Bavaria, scarcely differs at all in the wings from *Siphonurus*, except that the hind wings are appreciably larger. The gigantic May-fly nymphs from the fish shales of Siberia have also the characters of the Siphonuridæ, but differ from *Siphonurus* in having more double abdominal gills, herein agreeing better with Bengtsson's genus *Siphurella*. The venation of the adult, as shown by the Mongolian material, is more like that of *Ephemerella*, but also shows distinct affinity with the Permian *Prodromites*. The modern siphonurids will then constitute a subfamily Siphonurinae, in contrast with the gigantic Mesozoic Ephemeropsinae.

EPHEMEROPSIS Eichwald

Eichwald in 1864 founded the genus on an unfigured nymph from Siberia, which he called *E. trisetalis*. It came from the shales of the Transbaikal country, in the vicinity of Nertchinsk, north of the Gobi Desert. In 1868 the same author obtained a larger specimen from the same formation and vicinity and set it forth, with a figure, as *E. orientalis*. As Handlirsch remarks, this is very probably the same as *E. trisetalis*. Considerably earlier, in 1848, Müller had figured the tail of one of these nymphs in Middendorff's "Reise," the locality being Byrka, Siberia. Handlirsch bases his *E. middendorffi* on this figure but, except that the caudal appendages are said to be only about 15 mm. long (instead of 20

¹*Prodromites*, new name for *Prodromus* Sellards, 1907 (not Distant, 1904).

mm. or over), there is nothing to distinguish it. In 1889, Brauer, Redtenbacher and Ganglbauer figured a nymph from Turga, Siberia, which they considered to be *Ephemeropsis orientalis*. Handlirsch, on their account, founds a new generic name, *Phacelobranthus*, calling the species *P. braueri*. The genus is founded on the fact that the tracheal gills are beset with fine hairs, as in the siphonurid genus *Chirotonetes* Walker, which, however, has quite differently shaped gills. These hairs are seen only with difficulty and I cannot doubt that they exist in true *Ephemeropsis* as well. O. Reis (1910), in describing the fauna of the fish shales of the Transbaikal, figures *Ephemeropsis orientalis* with six pairs of double gills, the outer portion ciliated. The figure represents a "restoration" and in some details is not very accurate. Without having the original types, it is difficult to be positive about the actual characters of the four supposed species, but my present opinion is that they are all synonymous, and accordingly to be designated *Ephemeropsis trisetalis* Eichwald. Furthermore, I am not at present able to discern that the Ondai Sair species is separable from Eichwald's.

***Ephemeropsis trisetalis* Eichwald**

Plate I, Figures 1 to 9; Text Figures 2, 3, 4

NYMPH.—The one nearly complete Ondai Sair specimen is about 40 mm. long from front of thorax to base of caudal appendages (Pl. I, fig. 1). The thorax is about 13 mm. wide, thus considerably broader than in the Reis restoration, the body distinctly tapering posteriorly as in the figure of *Phacelobranthus*. I believe the last two pairs of gills are not double, but it is difficult to be sure that the inner lobe is not concealed beneath the abdomen (Pl. I, figs. 1, 2). The outer tapering lobe, resembling a slender knife blade in form, is about 5 mm. long, as described for *E. trisetalis* (Pl. I, fig. 3). The hind margins of the last two abdominal segments are laterally produced and pointed, as in the modern *Siphonurus*. This feature is not brought out by Reis, but it is better indicated in the figure of *Phacelobranthus*, though even here the projections of the last segment are not nearly long enough. The lateral caudal appendages are 23.5 mm. long; the middle one is evidently shorter, but my best specimen does not show the extreme tip (Pl. I, figs. 4, 5). I have been fortunate in finding nymphal wing pads, with venation as shown in the figures (Fig. 2 and Pl. I, figs. 6, 7). The drawing, figure 2, shows the branching of the radius (radial sector), about 6 mm. from base and 5 from apex of wing, and what looks like a faint cross vein from the lower branch to the vein below.



Fig. 2. Nymphal wing of *Ephemeropsis*.

WINGS.—Part of the adult wing has been preserved in one instance (Figs. 3, 4, and Pl. I, figs. 8, 9). It has the following characters: costa strongly arched at base, the strong oblique vein ending in the highest part (basal of this in *Ephemera*); sub-

costa normal, but at oblique vein very close to radius; radius (R_1) stout, practically parallel with subcosta; radial sector branching early, but not widely spreading, the upper branch forking about 7.5 mm. from its origin, the fork thus formed very narrow, its lower branch not elbowed, but doubling of cells beginning after the fourth; R_3 eventually widely divergent from R_4 (following Tillyard's nomenclature),¹ leaving a

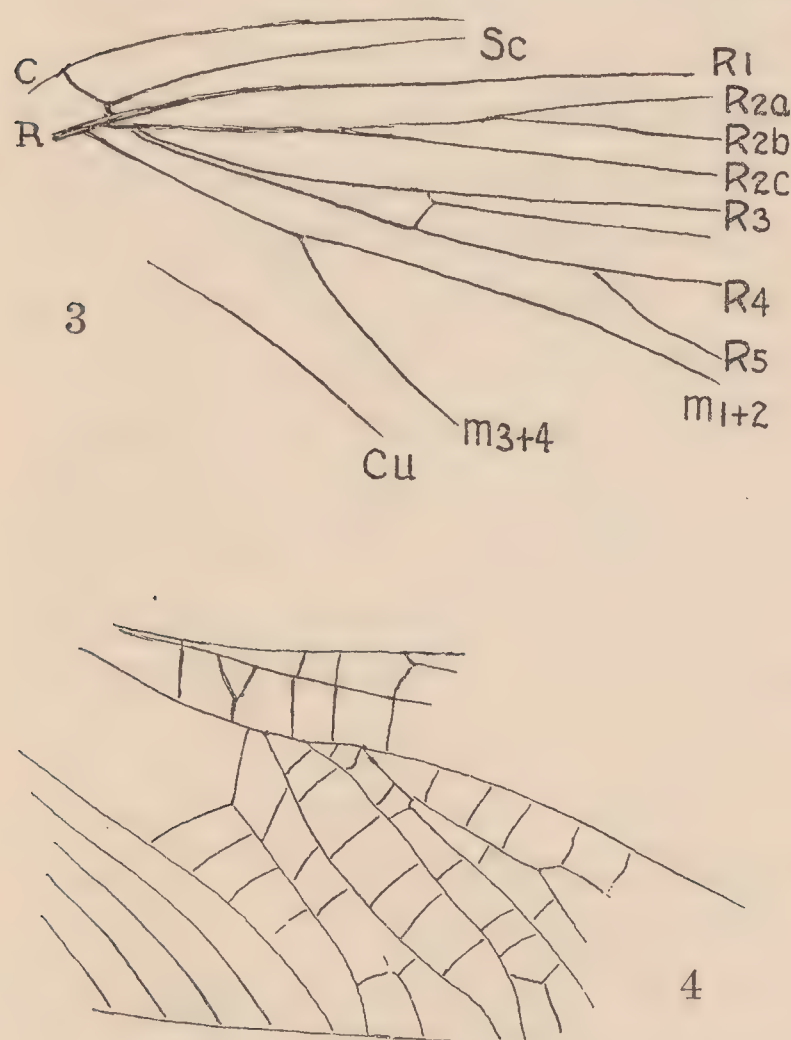


Fig. 3. Venation of the basal part of adult wing of *Ephemeropsis*: an analysis of the photograph, Plate I, Fig. 10.

C, costa; Sc, subcosta; R, radius; R_1 , 2, 3, 4, 5, branches of radius; Media, with branches m_{1+2} , m_{3+4} ; Cu, cubitus.

Fig. 4. Venation of part of the wing of *Ephemeropsis*. Compare with Plate I, Fig. 11.

large open reticulated area, with some supplementary longitudinal veins; R_{4+5} (M_{3+4} of Miss Anne Morgan) forking about 7.7 mm. from base of wing, the fork very wide, the lower branch most divergent but not elbowed at base, several supplementary longitudinal veins between the branches; first cubitus close to second, with no place for oblique veins to margin.

From the base of the main sector below appear to arise two branches, the one at the extreme base being the stem of the wide fork (supposed above to be R_{4+5}); the other, a little (1.3 mm.) farther along, is resolved on close inspection into two rather weak veins, practically contiguous, but after about 3 mm. gradually diverging, as shown in the figure. The uppermost of these veins again divides 4 mm. farther on, but the lower section is angulated basally, meeting a cross vein. The second or lower of these veins diverges widely apicad from the supposed R_4 and about 8 mm. from its origin branches again with a wide fork, the lower portion being so

The above description is based on the supposition that the wide fork so conspicuous in the specimen is actually the last radial fork of Tillyard, the medial fork of other authors. Difficulty arises, however, when we attempt an analysis of the radial branches, unfortunately somewhat disturbed by breakage. Leaving the wide fork out of the question, the radial branches lie close together, forking at extremely acute angles. The main branch of the sector is thicker and darker than the others and divides early, its upper branch again forking as described above.

¹Tillyard, 1923. Trans. New Zealand Institute, LIV, p. 227.

delicate as to appear like a supplementary vein. Now, if we assume that the conspicuous wide fork represents Tillyard's media (cubitus of Miss Morgan), then the weak fork above it and more apicad, although appearing doubtfully to belong to the primary venation, is the last fork of the radial sector, usually conspicuous in May-fly wings. On this basis, the veins above are all branches or divisions of R_2 , except the lowermost, which is R_3 . It then appears that R_3 arises from the sector at practically the same point as R_{4+5} , contrary to what we might expect, and contrary also to the condition in the Permian *Prodromites*. It is possible, however, to maintain that the closely adjacent veins arising from near the base of the sector are actually R_4 and R_5 , separate to base, the vein R_3 being placed as usual.

Very competent authors who have intensively studied the venation of May flies have already given us three quite different interpretations, so perhaps we may be excused if we hesitate to dogmatize about the homologies in *Ephemeropsis*. If the vein R_2 can present so many ramifications, other veins may also show unexpected complexity, and the determination of the basic scheme of venation becomes difficult. Certainly the wing pad of *Ephemeropsis* does not suggest that the complexities of the adult wing are directly derived from the primary veins.

It is proper to state that we have no absolute proof that the wing described belongs to the same species as the nymphs; but as it occurs with them and is of suitable size, I cannot doubt that it is identical.

HORIZON AND LOCALITY.—Ondai Sair formation (paper shales), Ondai Sair, Mongolia. The wing and wing pads were in the field parcel No. 79. The nearly entire nymph is in field parcel No. 64, but pieces of the same nymphs are also from parcel No. 79.

***Ephemeropsis melanurus*, new species**

Plate I, Figure 10

SPECIFIC CHARACTERS.—Abdominal gills 4.3 mm. long, double, both parts sharply pointed; the outer slender, curved below the middle; the inner broad, its width about 1.4 mm., caudal appendages fringed as in *E. trisetalis*, but much smaller, probably about 10 mm. long (about 8 mm. preserved), the appendages and their fringes black (fringes pale in *E. trisetalis*). The median tail at base is only about half a millimeter wide, while that of *E. trisetalis* is a full millimeter; but nevertheless at 7 mm. from base the tail with fringes is 2.5 mm. across, the fringes being very long.

HORIZON AND LOCALITY.—Ondai Sair formation (paper shales), Ondai Sair, Mongolia.

Although this specimen shows only the structures described, it is certainly a distinct species. Both the caudal appendages and the gills are sufficiently characteristic for recognition.

ODONATA

Æshnidæ

Cymatophlebiinæ (Cymatophlebiina Handlirsch)**CYMATOPHLEBIA** Deichmüller

This genus was based on a species from the lithographic stone of Solnhofen in Bavaria. A new figure was given by Needham (1907) in Bull. Amer. Mus. Nat. Hist., XXIII, p. 141. The Mongolian fossil is too incomplete for certain generic reference, but what there is agrees sufficiently with *Cymatophlebia*.

Cymatophlebia (?) **mongolica**, new species

Plate II, Figures 3, 4, 5

Costa and radius very stout; cells between costa and subcosta before nodus broader than high, thus much broader than in *C. longialata* (Germar); cells between subcosta and radius in same region similarly broad; radius in this region nearer to media than to subcosta; nodus as in *Cordulegaster*; costal cells beyond nodus broader than high; media branching at lower end of the very oblique subnodus; M_2 bent near base as if by a cross vein to R_5 , but I think this is merely a distortion. These characters are from the type, in parcel No. 64.

HORIZON AND LOCALITY.—Ondai Sair formation (paper shales), Ondai Sair, Mongolia.

Another specimen (also with No. 64) shows the nodus and part of the region just beyond. It is so much distorted that it looks like another species, M_1 being under the radius, and the end of the subcosta thrust upward. It is of value only as showing an early duplication of cells between M_1 and M_2 , a character of *Cymatophlebia*, only whereas in the latter the paired cells are about equal, in our fossil the first few paired cells show the upper one very large and the lower very small, hardly a fifth the size of the upper. More apicad, the cells rapidly become subequal. Still another specimen (field label No. 79) shows part of the sub-basal region of wing and indicates the presence of high narrow cells in the hind wing, the lower portion folded over and much confused.

TRICHOPTERA

TRICHOPTERELLA, new genus

GENERIC CHARACTERS.—Size medium; wings broad; costal margin very gently arched, slightly concave near base; radius (R_1) straight to R_1 - R_2 cross vein, then arched upward, resuming a direct course at a higher level; radial sector arising near base of wing, branching to form a long discoidal cell, the base of which is more acute than the base of the first fork; cross vein at end of discoidal cell somewhat oblique; separation of R_2 from R_3 a short distance before end of discoidal cell, of

R_4 and R_5 just beyond discoidal cell; no R-M cross vein; media apparently with only two branches, but the ends of these are obliterated and it is not impossible that they forked near the apical margin; fork of media at about same level as fork of R_4 and R_5 ; M-Cu cross vein obliquely arising from media a little before the fork and joining the cubitus at the fork or very slightly before it; first anal straight to end, parallel with and remote from second; postcosta or second anal forming with the others the usual pointed cell, enclosing a smaller cell toward base. Only the anterior wing is known.

***Trichopterella torta*, new species**

Figure 5

SPECIFIC CHARACTERS.—Anterior wing 15.5 mm. long, 6 mm. wide; veins pale brown, no markings preserved; discoidal cell 3.8 mm. long; R_5 branching 5.7 mm. from base of wing; long anal cell ending 5 mm. from base of wing; length of cubital fork 4 mm.

HORIZON AND LOCALITY.—Ondai Sair formation (paper shales), Ondai Sair, Mongolia. In parcel No. 64.



Fig. 5. Discoidal cell of wing of *Trichopterella torta*.

The numerous Trichoptera from the Lias are all small, the anterior wings ranging from 3.2 to 9 mm. long, only one species exceeding 5 mm. Two of the Lias genera, also represented by small species, occur in the Jurassic. The entirely separate and parallel-running first anal of *Trichopterella* is equally seen among the Lias genera, such as *Necrotaulius*, *Mesotrichopteridium* and *Pseudorthophlebia*. All these insects, however, have the characteristic anal cells, which are lacking in Tillyard's Mesopsychoidea (four genera) from the Upper Triassic of Queensland.

On the other hand, *Trichopterella* seems to be specialized, after the manner of the Tertiary and modern *Setodes*, in the reduction of the media to two simple branches; but it is not impossible that these were forked near the margin. The media and cubitus of *Trichopterella* separate very early, at the same level as the origin of the radial sector, hence the cellula thyridii is very long, nearly twice as long as the discoidal.

There is a rather wide crack in the rock across the middle of the wing, but this does not obscure the venation.

There is one Jurassic genus, *Mesotaulius* of Handlirsch, from the lithographic stone of Bavaria, which has the anterior wings 31 mm. long. It has little affinity with *Trichopterella*.

The living genus *Alepomyia* Banks from Newfoundland has a two-branched media, but is otherwise quite distinct from *Trichopterella*.

Reis recorded a trichopterous larva case from the fish shales of the Transbaikal. A similar or identical species occurs in the Ondai Sair shales, as follows:

***Indusia reisi*, new species**

Plate II, Figure 10, on the stem of *Phyllocladites*

SPECIFIC CHARACTERS.—A larva case was found contiguous with the base of a specimen of *Phyllocladites morrisi*. It is cylindrical, straight, very broad, composed of grains of sand, and similar to that of the modern genus *Stenophylax*. On the east side of the main draw, half way between Uskuk and Hsanda Gol, F. K. Morris found a heavy slab, about 15 mm. thick, showing numerous specimens of *Estheria middendorffi* and a few caddis cases on one side, and on the other very numerous caddis cases. From this additional material it can be determined that *Indusia reisi* cases are sometimes as much as 22 mm. long, very slightly curved, 2 mm. diameter at the little end, 3.7 at the larger. The distinct pebbles are mainly at the larger end, the choice of materials varying with age, as in *Stenophylax*. The case figured by Reis was ornamented with ostracods.

HORIZON AND LOCALITY.—Ondai Sair formation (paper shales), Ondai Sair, Mongolia.

DIPTERA

Chironomidæ

CHIRONOMOPSIS Handlirsch

This genus was based on *Chironomus arrogans* Giebel, a name founded on Brodie's figure of a supposed *Chironomus* from the English Purbeck. It shows no distinct generic characters and I have used the name only in a general sense, as applicable to fossil Chironomidæ of uncertain status.

***Chironomopsis gobiensis*, new species**

Plate II, Figures 6, 7

SPECIFIC CHARACTERS.—Female. Length about 7 mm.; head small, with large eyes; antennæ long and slender, with cylindrical joints, longer than broad, not visibly hairy; palpi extended, about half as long as antennæ; thorax elevated, gibbous anteriorly; legs long, tibiæ apparently longer than femora, hind tibiæ about or nearly 3 mm. long. Color as preserved, brown, evidently dark brown or blackish in life.

HORIZON AND LOCALITY.—Ondai Sair formation (paper shales), Ondai Sair, Mongolia. In parcel No. 79.

Several specimens, apparently referable to a single species, have been found. So far as visible, the antennæ and mouth parts strongly suggest the bloodsucking *Culicoides* group, but it would be going too far to affirm distinctly that this is a bloodsucking form. It is possible that

the bloodsucking habit among Diptera arose without reference to the Mammalia, as *Simulium* is known to attack young fish and Culicidæ have been seen to prey on cold-blooded vertebrates, reptiles and amphibians. Thus the opportunities for the development of such habits presumably existed before there were any Diptera.

C. gobiensis is evidently the species reported as "mosquitoes," but I think it is practically certain that it does not belong to the Culicidæ. It is very different from *Mesopsychoa dasyptera* Brauer, Redtenbacher and Ganglbauer, from the Jurassic of Ust Balei, Siberia.

COLEOPTERA

There are two or three species of beetles in the Ondai Sair collection, but their preservation is so poor that I do not venture to describe them (Pl. II, fig. 8). The *Carabites latecostatus* of Reis is certainly not represented.

PLANTS

GINKGOALES?

Baiera furcata (Lindley and Hutton)

Plate II, Figure 9

The plant remains in the Ondai Sair shales are fragmentary and not readily referable to particular species. There is, however, one specimen which, so far as it goes, appears to agree exactly with *Baiera furcata* (Lindley and Hutton) Braun, which Seward calls *B. lindleyana* (Schimper), disregarding priority. This *B. furcata*, or fossils indistinguishable from it, may be either Jurassic or Lower Cretaceous. Seward states that it is known from the Middle Jurassic of Chinese Dzungaria; he is also disposed to refer to it the plant from the Lower Cretaceous of the Black Hills, which Fontaine recorded as *Czekanowskia nervosa* Heer. *Baiera* is in general highly characteristic of the Jurassic but rare in the Lower Cretaceous.

From the Siberian Jurassic, Heer recorded a *Trichopitys setacea*. The genus *Trichopitys* of Saporta, with *Baiera*-like foliage, was originally based on a plant from the Permian, which appears to be related to the Ginkgoales. Seward has suggested that *T. setacea* does not belong to the Permian genus, but is to be compared with *Baiera lindleyana*.

In the Ondai Sair shales are robust shoots bearing stalked obpyriform bodies more or less comparable with the fruits of *Trichopitys heteromorpha* as figured by Zeiller. In one specimen, at least, there is a distinct seedlike impression at the base, and on closer analysis there seems to be

nothing to separate the species from *Phyllocladites* Heer (*Drepanolepis* Nathorst), which occurs in the Jurassic of Spitzbergen. Seward defines the genus as consisting of strobili of open habit with single-seeded sporophylls, of uncertain systematic position but probably gymnospermous. The general resemblance to the fruiting shoots of the Ginkgoales is sufficiently close to suggest a possibility that these are after all the fruits of *Baiera furcata*, or at least belong with the foliage which cannot be separated from the latter species. There is, however, some indication of possible narrow bract scales, suggesting remote affinity with *Larix*. It seems desirable to give this organism a name, so it may be introduced as follows:

***Phyllocladites* (?) *morrissi*, new species**

Plate II, Figures 10, 11; Text Figure 6

SPECIFIC CHARACTERS.—Stout erect shoots, at least two inches long, the straight stiff stem about 2 mm. wide about 35 mm. from apex; sporophylls on short stout stalks about 2 mm. long. Sporophylls 6 to 7 mm. long, about 3.5 wide near base, obpyriform, with very obtuse apex. Ovules or seeds circular.

HORIZON AND LOCALITY.—Ondai Sair formation (paper shales), Ondai Sair, Mongolia. In parcel No. 64.

Named after Mr. Frederick K. Morris, who collected the material.

I sent a sketch of this plant to Dr. E. W. Berry; he kindly replied that he was not able to place it with any species known to him.



Fig. 6. *Phyllocladites morrissi*.

***Czekanowskia* species**

Four contiguous broad-linear (1.5 mm. diameter) leaves, the portion preserved 56 mm. long, resemble pine needles, but apparently belong to *Czekanowskia*. It is impossible to refer them to any particular species.

Ondai Sair formation, "No. 64, Ondai Sair."

Reis has figured similar leaves, but apparently more slender, from Turga. He referred them to *Czekanowskia* sp. The genus is characteristic of Jurassic strata, but is reported from the North American Cretaceous.

PLATES I AND II

PLATE I

Figs. 1-9. *Ephemeropsis trisetalis* Eichwald.

Fig. 1. Nearly complete nymph about 40 mm. long.

Fig. 2. Part of a nymph, showing legs and abdominal gills.

Fig. 3. Abdominal gills, detached from the nymph.

Figs. 4, 5. Caudal appendages of nymph.

Figs. 6, 7. Nymphal wing pads.

Figs. 8, 9. Adult wing, basal portion.

Fig. 10. *Ephemeropsis melanurus*, new species. Detached gills and caudal appendages.

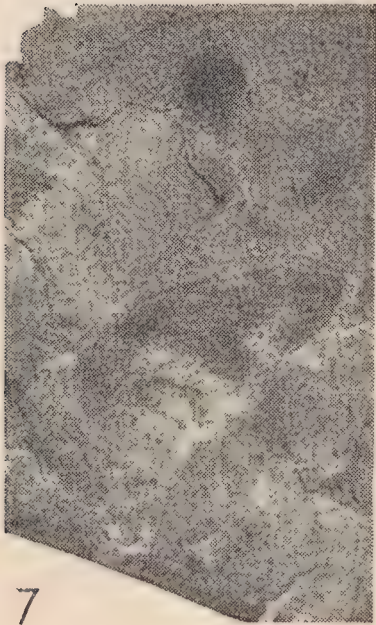
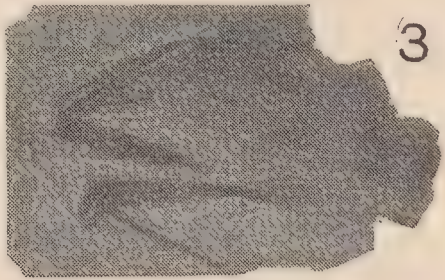
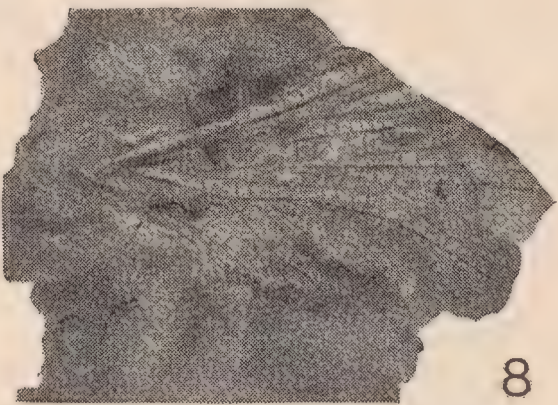
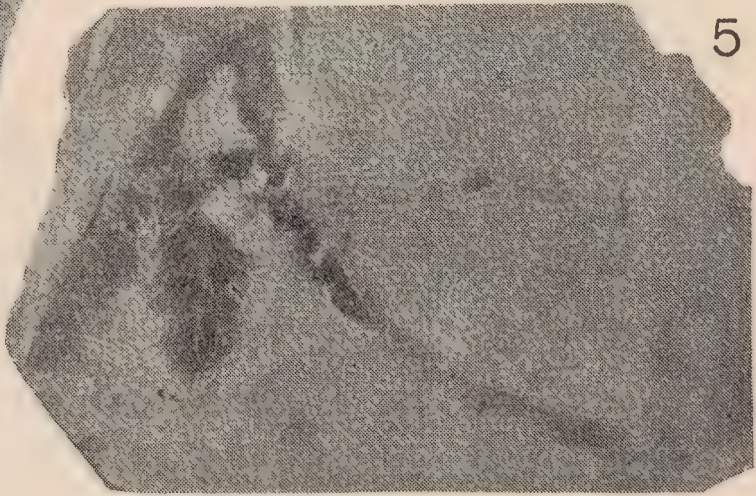
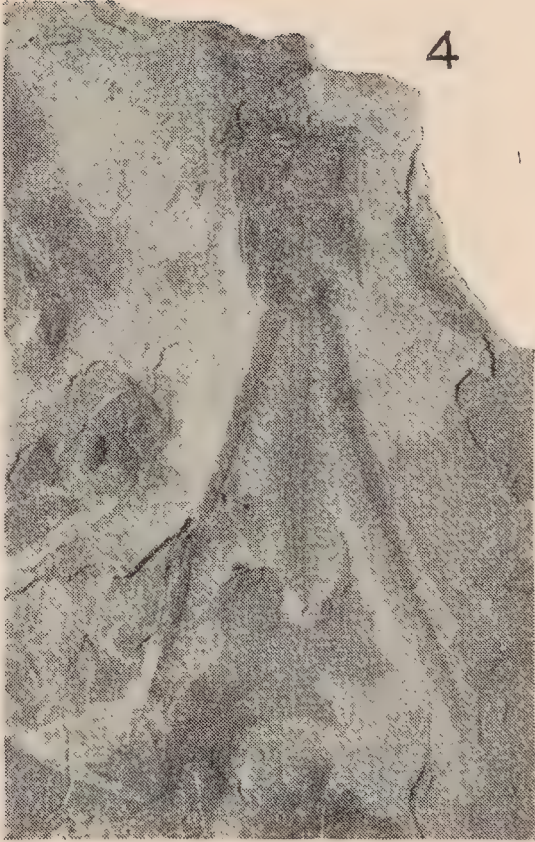


PLATE II

Fig. 1. *Lycoptera middendorffi* Johannes Müller.

Fig. 2. *Estheria middendorffi* T. R. Jones.

Figs. 3, 4. 5. *Cymatophlebia* (?) *mongolica*, new species. Details of wing.

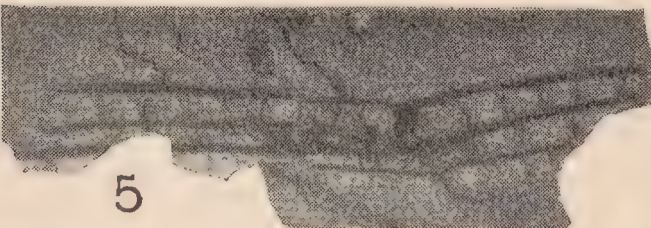
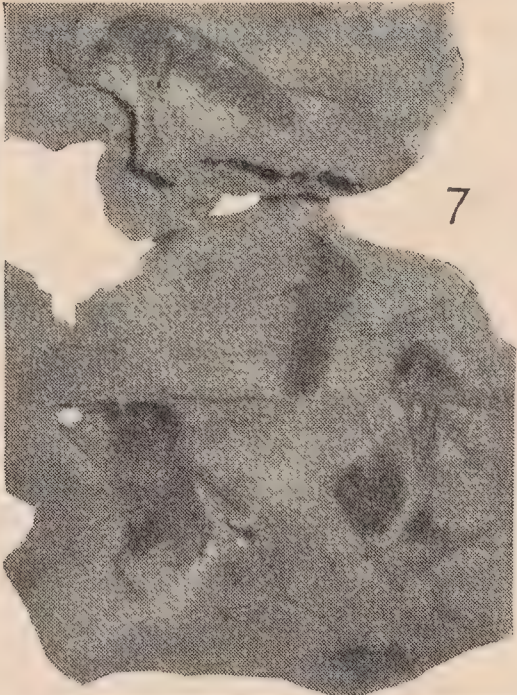
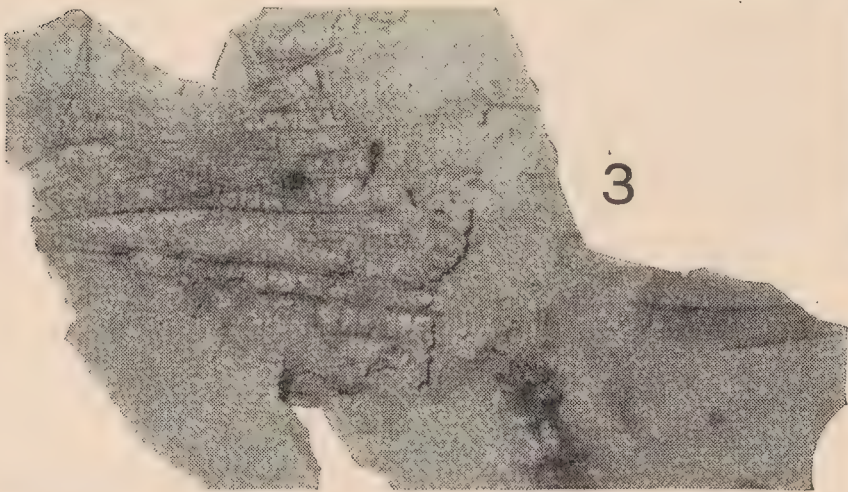
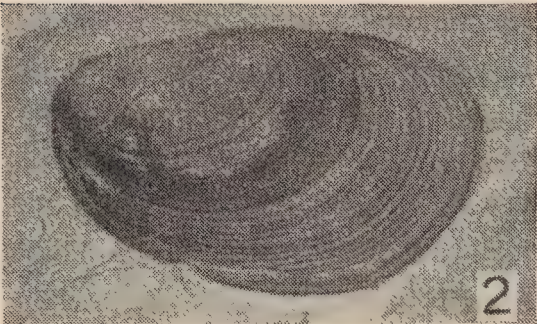
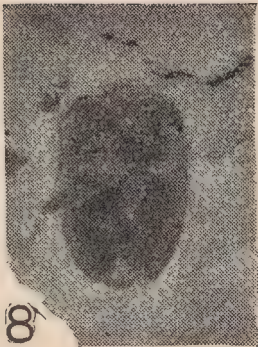
Figs. 6, 7. *Chironomopsis gobiensis*, new species.

Fig. 8. Beetle, undetermined.

Fig. 9. *Baiera*.

Figs. 10, 11. *Phyllocladites* (?) *morrissi*, new species. Near the base of Fig. 10 specimen is the caddis case of *Indusia reisi*, new species, touching the stem of *Phyllocladites*.

Fig. 12. Plant, undetermined.



Article VII.—THE PECTORAL LIMB OF *ERYOPS* AND OTHER PRIMITIVE TETRAPODS

BY ROY WALDO MINER

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INTRODUCTION

It is generally agreed that the primitive tetrapod is a direct evolution from an original fishlike ancestor, and there seems no doubt that this primitive tetrapod was an amphibian. The members of this group retain fishlike characters possessed by no other group of tetrapods, and among them are the most generalized four-footed animals.

There is strong evidence that the early Amphibia gave rise to the most primitive reptilian groups, and there seems no serious question, at the present day, that the birds and mammals are offshoots from the reptilian stem. It is even possible to postulate that the origin of the first reptiles may be looked for in the group Stegocephalia among the Amphibia; while the birds unquestionably arose from some swift-moving, light-boned diapsid type, and the paleontological evidence that the cynodont reptiles gave rise to the primitive mammals has been greatly strengthened in recent years. In all these cases there are transitional types which, from the standpoint of paleontology and comparative anatomy, give a reasonable explanation for the origin of many of the most characteristic structures typical of the various tetrapod classes, which in many cases is strengthened by embryological data.

Between the most primitive Amphibia, however, and the original fish ancestor, there is a more serious gap. The fishlike segmentation of the amphibian body musculature, the possession in most forms of functional gills and gill slits at least at some time in the life history, the intermediate condition of the heart and circulatory system in general, the brain, the survival of lateral line organs, the arrangement of the dermal and cartilaginous bones of the skull, the presence of dermal scales, and many other anatomical and physiological features, bespeak a fish ancestry for the group; but the origin of the pentadactyl tetrapod limb is not well known. No transitional types leading to its essential structure exist, and yet no comparative anatomist of today can deny its ultimate origin from the paired fins of fishes. Clear indications of the piscine origin of the early amphibian shoulder girdle are to be seen in such structures as the cleithrum and primitive clavicle of the stegocephalian amphibian; but the limb itself, with its humerus, radius, ulna, carpals, metacarpals and phalanges, may as yet be only categorically referred to their probable origin in a hypertrophy and rearrangement of certain basal fin elements of the crossopterygian ganoid, the fish type which in other respects most nearly suggests an approach to amphibian ancestry.

We have, then, in the primitive amphibian a creature that evolved from a fishlike ancestor, but in the full possession of a typical digitated limb, articulating from a girdle betraying its piscine origin, but separated by a considerable gap from the true fish-fin. On the other hand, we have in the amphibian tetrapod limb the most primitive structure of this kind among the higher animals. Its musculature is fundamental to that of the higher types, and a clear understanding of its structure and arrangement is essential in interpreting the manifold changes which have taken place in the limb muscles of the various tetrapod classes and orders. It will also give the nearest approach to the fundamental musculature of the paired fish-fin. Should fossil transitional forms at some time be found, the relationship between the musculature and skeleton of the amphibian limb would be helpful in interpreting its significance, and, since the earliest stegocephalian amphibian is by far the most primitive tetrapod, it is clear that a knowledge of its musculature, could it be gained, would be of great importance. The remains of the Stegocephalia, though abundant, are naturally skeletal in their nature, and, at first sight, it would seem impossible to arrive at even an approximately accurate idea of their musculature. Nevertheless, we know from the physiological processes of bone formation, that the vertebrate skeleton is deposited in the form of cartilage or carbonate of lime, or both, in the interstices of the connective tissue network which also encloses the contractile muscle cells. It is obvious that these hard, skeletal deposits cannot exist where they would interfere with muscle action, and, conversely, it is evident that they would occur in most highly developed condition where they would assist and strengthen that action. The areas of lost motion between opposing muscle groups would best answer this purpose, and it is in such inter-muscular fibrous regions of connective tissues that the fundamental internal bony or cartilaginous skeleton is found. In the course of time, this was combined with bony protective plates on the outer surface of the body, which, through underlying connective tissue strata, are connected with muscle areas, and the two systems of rigid structures were welded into a framework where customary muscle contraction most required it.¹

The vertebrate endoskeleton may, therefore, be said to have been extensively molded by muscle activity, and its form to the smallest detail often shows indications of this fundamental influence. If, therefore, the skeleton of vertebrate types is studied in conjunction with the muscular and connective tissue systems and interpreted from this light, much can

¹The skull conspicuously illustrates this principle, for it is composed of a series of arches braced mechanically against the pulls and stresses of vigorous jaw and trunk muscles.

be inferred, conversely, regarding the original musculature of fossil types by an intelligent study of their skeletal remains, especially if careful comparisons are made with the skeletons of the most nearly related living forms.

In this paper an attempt has been made, first, to restore the pectoral girdle and limb of a primitive amphibian tetrapod of the stegocephalian group, and, by a careful comparison of the musculature of a primitive living amphibian with that of a living reptile in relation to the skeletal structure, to infer the typical stegocephalian musculature of this region and interpret it with especial regard to its character as the fundamental anterior limb musculature of the tetrapods as a whole. The species *Eryops megacephalus* Cope has been chosen for restoration: first, because it is one of the most typical of the Stegocephalia; second, because of the abundance of its fossil remains; third, because of its large size and, consequently, the comparative ease with which the characters of the skeleton and the surface indications of the muscle attachments may be made out; fourth, because of the very complete ossification of the skeleton, which makes it unnecessary to restore hypothetically large areas of cartilaginous skeleton, and, to a corresponding degree, renders more certain the size, shape and articulation of the comparatively small cartilages that must be inferred; finally, because it is evident that it has not been greatly specialized either for an aquatic habitat or for any restricted terrestrial habit of life.

Hence, it exhibits a generalized condition of fundamental importance as indicating a center of anatomical radiation for the skeletal and muscular systems of all the later specialized and more closely adapted vertebrate groups. A clear understanding of its structure is thus of the greatest significance in throwing light upon the origin and evolution of the morphology of present-day vertebrates, as contrasted with the former custom of selecting specialized modern types for this purpose.

The pectoral girdle and limb have been chosen for this study, partly because of the necessity for a limit to the inquiry, partly because their evolution is typical of that of the locomotor mechanism as a whole, and partly because of various interesting problems which have arisen in connection with the later history of the limb along both the amphibian and the reptilian lines.

Much has been written regarding a possible "serial homology" between the various bones and muscles of the pectoral and pelvic systems. This question, though interesting, is so complicated, and many of its aspects are so doubtful, that it will not be touched upon in this paper,

other than to record the writer's impression that the many similarities, close as they often appear to be, are probably the result of parallel evolution of two systems of similar origin undergoing progressive adaptive changes, under similar conditions.

This paper, therefore, will be confined entirely to a consideration of the fundamental vertebrate skeleton and musculature of the pectoral girdle and limb and their bearing on the evolution of later types.

The jaw muscles of vertebrates have been treated in a similar way in a valuable paper by L. A. Adams (1919), while W. K. Gregory and C. L. Camp (1918) have shown the value of utilizing primitive types for interpreting the musculature of modern forms by their study of the skeleton and inferred musculature of *Cynognathus*, as a basis for analyzing the evolution of the fundamental mammalian musculature. In this work, however, they adopted the homologies of Fürbringer and Gadow for reptilian and mammalian musculature. A. S. Romer (1922) has carried this work further and has established a more exact basis of homology by comparing modern reptilian and mammalian musculature and skeletal features with the skeletal features of a large series of fossil reptiles, and has succeeded in throwing considerable light on the chief features of mammalian muscle systems as evolved from reptilian prototypes.

The present paper aims to emphasize the splitting of the generalized stegocephalian musculature into that characteristic of the primitive amphibia as distinguished from the musculature of the primitive reptiles, contrasting the basic features of the pectoral limb musculature of each, with especial reference to the evolution of the amphibian type of muscle arrangement as distinguished from that of reptiles.

The method of investigation has been as follows: Because of the established ancestral relationship of the Stegocephalia as a group to both the amphibian and the reptilian stems, (1) the fossil remains of a typical stegocephalian limb skeleton were restored, reassembled and compared with the limb skeletons of the most generalized living reptile and one of the most generalized living amphibians, and the undoubted skeletal homologies noted. (2) The pectoral limb musculature of the two recent types was dissected, and its relations to the respective skeletal features noted. (3) The amphibian musculature was then homologized as far as possible with that of the reptile, using as criteria the location of the basic muscle systems; their relations to each other and to the bones; their position with reference to the chief nerve trunks and blood vessels, and, especially, to the principal intermuscular connective tissue areas; their origins and insertions, and, finally, their innervations. (4) An endeavor

was then made to infer the ancestral stegocephalian musculature, by assuming that homologous muscles in both groups would be represented in their common ancestral stock; that the origins and insertions of this musculature would be largely determined, first, by surface features on the ancestral skeleton homologous to those on the recent amphibian and reptilian girdle and limb bones, and, second, by assembling the fossil skeleton as nearly as possible in its original position; that the chief differences between the recent and fossil skeletons would also give a clue to corresponding differences between recent and stegocephalian musculature; and that the chief differences between recent reptilian and amphibian musculature might be explained by comparing them simultaneously, in connection with the correlated skeletal features with a limb skeleton representative of their common ancestral type and its inferred musculature. (5) These observations were checked by a comparison with other fossil material and modern types, by considering the work of other investigators and by giving due weight to embryological data so far as they are known.

During the course of the work an attempt was made to reassemble the shoulder girdle of *Eryops* in relation to the axial skeleton, and, by a restoration of the musculature, to arrive at the muscular action of the anterior part of the animal and its probable appearance in life.

An attempt has been made to solve several of the moot questions regarding *Eryops*, as well as the evolution of certain problematic amphibian features.

The recent types chosen for comparison are *Sphenodon punctatus* (Gray) of New Zealand, and *Megalobatrachus maximus* (Schlegel) of Japan. The works of Fürbringer (1900) and Osawa (1898, 1902) have been freely consulted in connection with their dissection, and several differences noted between my own opinions and interpretations and those of these authors. The opportunity has also been utilized to present clearer figures of certain features of dissection than have hitherto been published, and to figure others which have never been illustrated.

As is well known, the genus *Sphenodon* is a very ancient type, belonging to the group Rhynchocephalia, with fossil representatives reaching back to mid-Triassic times. The only living species possesses, on the whole, the most generalized skeleton and musculature of all known living reptiles, and it is practically a "living fossil."

Megalobatrachus japonicus (Schlegel), until recently grouped with *Cryptobranchus alleganiensis* (Daudin), is now considered to be generically separate. It is the largest known urodele, and, together with

Cryptobranchus and the primitive hynobiids (Noble, 1922; Dunn, 1922), exhibits what is probably the most primitive musculature of living Amphibia. It shows considerable adaptation to life in the water, but its cenotelic characters are readily detected and have to do mostly with general body form and a greater development of cartilaginous skeleton, or rather, what amounts to the same thing, a very incomplete ossification.

I wish to acknowledge especially the great assistance derived from the various works of Fürbringer (1873–1900) on reptilian and amphibian shoulder musculature, as well as those of Osawa (1898, 1902), Ribbing (1907), Rabl (1901), Siegelbaur (1904–1909), Wilder (1903–1912) and McMurrich (1903–1920). I wish to acknowledge my indebtedness to the paleontological works of Abel (1919), Case (1900–1915), Williston (1910–1920) and Moodie (1909–1916), and to express my admiration for the excellent work of Professor D. M. S. Watson (1917a) on the evolution of the tetrapod shoulder girdle and the classification of primitive tetrapods.

Especial thanks are due to The American Museum of Natural History for the use of the collections; to President Henry Fairfield Osborn, Director F. A. Lucas and Curator W. D. Matthew for many courtesies extended to me; to Dr. A. S. Romer and Dr. G. K. Noble for critical discussions and valuable suggestions during the final revision of the manuscript, and, finally, but particularly, to Dr. W. K. Gregory for the inspiring interest and enthusiastic support he has given me in connection with the whole work and for his invaluable aid and advice during its gradual evolution.

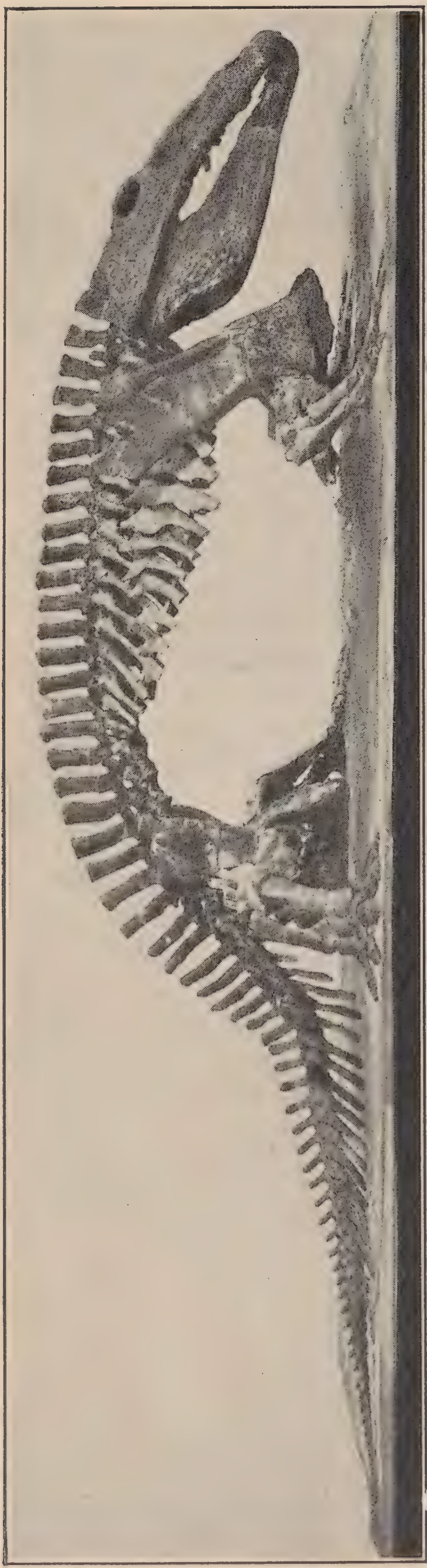


Fig. 1.—Mounted specimen of *Eryops megacephalus* in The American Museum of Natural History, showing right side.

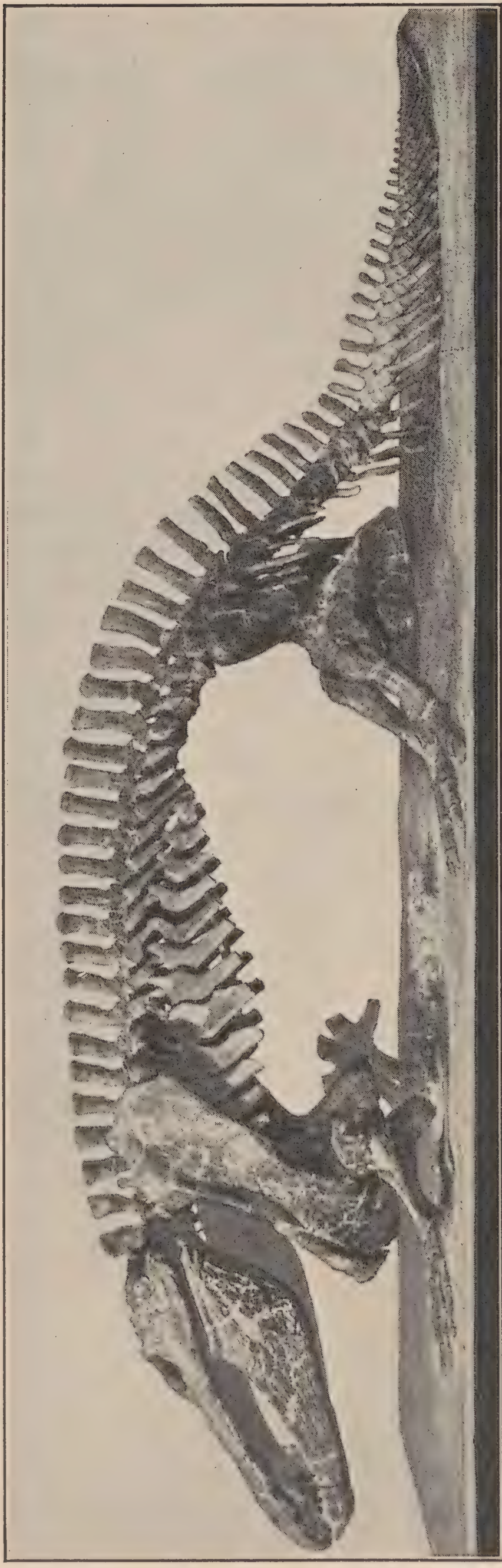


Fig. 2.—Same as figure 1, showing left side.

SECTION I. PECTORAL SKELETON

A. SHOULDER GIRDLE

a. The Shoulder Girdle of *Eryops*

General Description of Eryops.—The chief skeletal remains of *Eryops* have been derived from the Permian deposits of Texas and Oklahoma, where the species *Eryops megacephalus* is abundantly represented. It is also known from the Permian of Kansas and Illinois (Case, 1915, p. 127) and doubtfully from New Mexico. Case has found vertebral remains in the Upper Pennsylvanian of Pittsburgh, Pennsylvania, which he assigns to the genus *Eryops*. Hence the range of the genus may be said to extend from the Upper Carboniferous through the Permian.

The fossils thus far found include practically the entire skeleton, of which a nearly complete specimen is shown restored in the American Museum of Natural History (Figs. 1, 2, 4). Numerous skulls of remarkable completeness are known, and separate limb bones and vertebræ are frequent, of which the richest collections are those of the American Museum of Natural History, the Walker Museum at the University of Chicago, and the Museum of the University of Michigan.

Eryops is the largest known Permian amphibian (Case, 1915), reaching more than six feet in length, with massive solid-roofed skull of the stegocephalian type (Fig. 4), elongate powerful jaws, well equipped with conical pleurodont teeth of irregular size, as usual in animals having carnivorous habits of feeding. The eye sockets, set posteriorly and toward the summit of the skull, are in the position characteristic of animals accustomed to a partly submerged habit of life, though the powerfully built limb bones, capable of supporting the weight of the body, betray a capacity for terrestrial locomotion. *Eryops* doubtless lived in comparatively shallow waters on the margin of swampy lakes and streams, as shown by the geological character of the deposits in the region where it lived and pursued its prey. Coprolites found in the vicinity of its remains, if referable to *Eryops*, would indicate that its food included fish and smaller amphibians (Case, 1915).

The massive pectoral girdle (Figs. 3, 7, 10, 15) consists of paired scapulocoracoids, clavicles and a single median interclavicle. The scapular blade is equipped with a well-developed cleithrum.

The pectoral limb bones (Figs. 7, 18, 21) comprise a short, massive humerus, short radius and ulna, a well-ossified carpus, consisting of eleven carpal bones, four digits and a prepollex, with short metacarpals and phalanges. The latter, though not completely known, probably possessed the formula, 2.2.3.2.

These elements will now be described in detail.

Scapulocoracoid.—The scapulocoracoid (Fig. 3) is a heavy single bone, there being no evidence of a suture separating it into scapular and coracoid elements. The greater portion consists of the elongate scapular blade extending vertically, while the ventral coracoidal portion is a comparatively small region with rounded border. On the anterior border of the scapula there is a moderately well-developed cleithrum, a membrane bone with a slender stem ventrally and an expanded portion dorsally, which overlaps the dorsal end of the scapula and tapers to a curving point at the upper posterior angle.

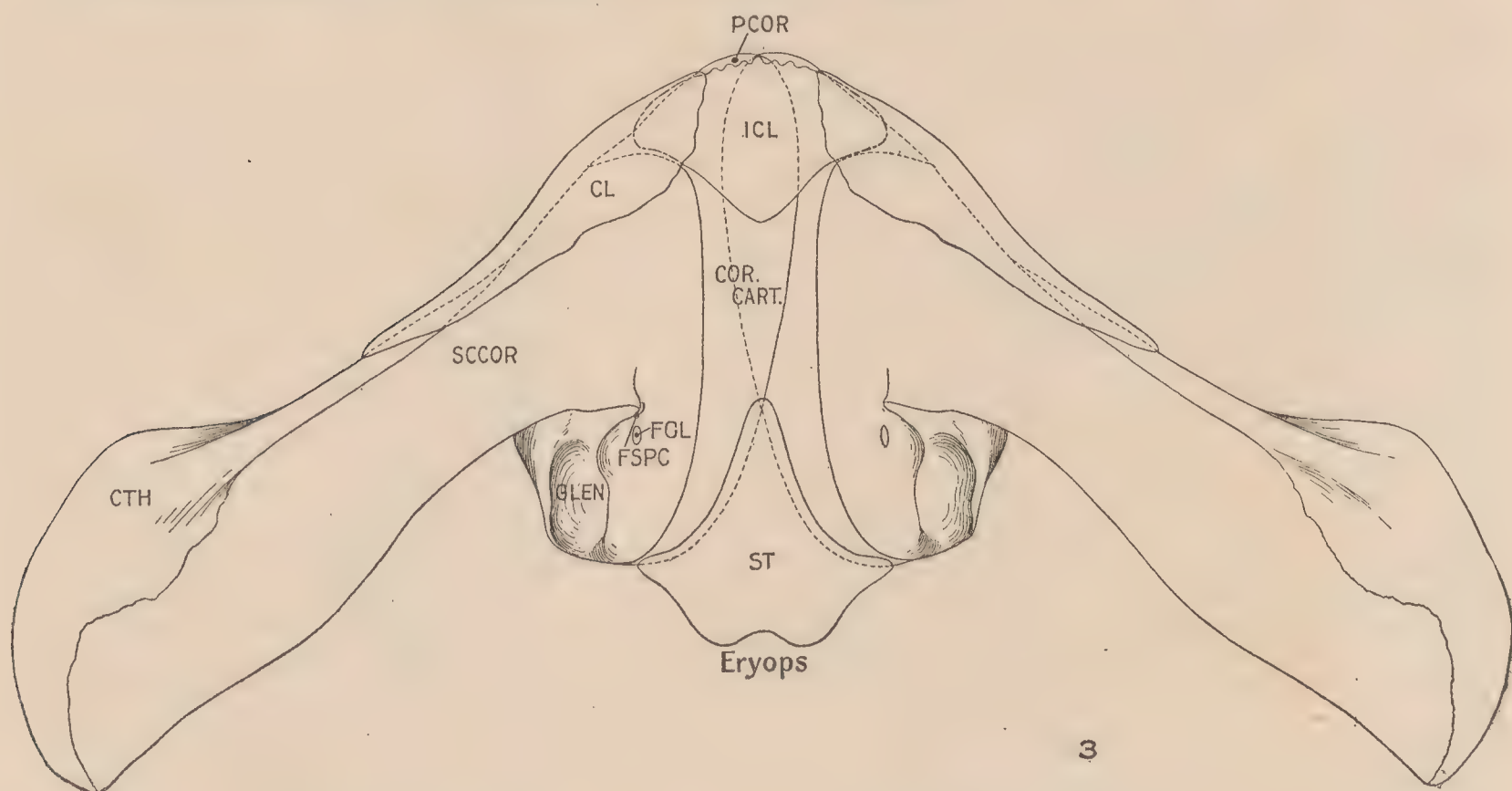


Fig. 3.—Restoration of the shoulder girdle of *Eryops*, with elements in their proper relations, but represented as if in one plane.

Note that the clavicles are separated from each other on the median line, and thus do not overlap. The coracoid cartilage (COR. CART.) and sternum (ST) are inferred and separate the scapulocoracoids.

The comparatively small coracoidal portion is mostly anterior to the glenoid cavity, with a much smaller extension posterior and ventral to the glenoid. It is pierced by the supracoracoid and glenoid foramina, just ventrally to the anterior part of the glenoid cavity. It is worthy of note that the greater expanse of the coracoid is situated anterior to the supracoracoid foramen.

The medial margin of the coracoid is marked around the thickness of its edge by a shallow groove that extends from well around the antero-medial border to a point just back of its posterior curve, terminating a short distance below the posterior limit of the glenoid. This marks the articulation with the cartilaginous portion of the coracoid, which is, of course, not preserved in the fossil specimens.



Fig. 4.—Mounted specimen of *Eryops megacephalus* in The American Museum of Natural History. Dorsal view.

The scapulocoracoid is braced on the inner side by the heavily ossified supraglenoid buttress, spanning the oval, tunnel-like supraglenoid foramen at the junction of the scapular and coracoid regions (Figs. 10 and 11). This arch extends upward as a strong buttress on the inner side of the scapular blade, while its lower extremity curves medially and posteriorly to form the posterior border of the coracoid. On the outer face the base of the scapular portion terminates in a boss-shaped process which forms the anterior or scapular limit of the glenoid cavity, the posterior part of which is excavated out of the posterolateral surface of the supraglenoid buttress which embraces it from behind. It is thus framed in between these two features of the bone.

The glenoid cavity is "screw-shaped" and elongate. It runs in an anteroposterior direction. Its form and relations to the scapula and supraglenoid buttress are shown in figures 3, 11 and 15. It will be further described in considering the articulation of the humerus.

Immediately posterior to the glenoid cavity on the hinder edge of the coracoid, is an excavated triangular area (Fig. 11 E), which is in the proper position to serve as the attachment for the coracoid head of the anconæus muscle.

Just below the supraglenoid buttress there is a triangular pit, the subscapular fossa, within which lie the inner openings of the supraglenoid and supracoracoid foramina. At the junction of the supraglenoid buttress with the internal coracoidal surface is the inner aperture of another foramen which opens on the outer surface of the coracoid in a depression posterior to the supracoracoid foramen and below the center of the glenoid cavity. This has been termed the glenoid foramen (Williston, 1909).

Clavicle.—The clavicle (Figs. 3, 15), like the cleithrum, is a membrane bone, as indicated by its sculptured outer surface. Dorsally, it overlaps the anterolateral surface of the ventral stem of the cleithrum, following the lower anterior border of the scapulocoracoid. It is somewhat narrowed dorsally, but it expands ventrally to form a thin tapering plate, strengthened by a rounded ridge along its outer median surface. It tapers to a blunt point at the ventral terminus where its surface is ornamented by low, fluted ridges. Ventromedially, it extends beyond and anterior to the scapulocoracoid, and articulates with the interclavicle in the manner shown in figure 3, as will be explained below. At about two-thirds of its extent, ventrally, it shows a slight bend, forming a low boss at an angle of about 150 degrees. Several clavicles have been found bent at varying angles nearly approaching a right angle, as in the

articulated girdle (No. 4186, A. M. N. H.) described and figured by Cope (1888) and by Case (1911) but these give clear evidences of having been bent and crushed out of shape. A pair of clavicles in the American Museum (No. 4307), although broken, have perfect contact surfaces and are uncrushed. They doubtless show the correct angle and also to a large extent the surface sculpture.

Interclavicle.—The interclavicle (Figs. 3, 10, 15) is a median membrane bone, rhomboid, or rather fan-shaped in outline, sculptured on its lower surface, although the girdle figured by Cope, above mentioned, possesses an interclavicle sculptured visibly only at its anteromedian edge, where it shows a number of toothlike projections. These appear to be about seven in number, the median one being the longest.

Restoration of the Shoulder Girdle (Figs. 3, 7, 10, 15).—The fossil remains of the shoulder girdle are so complete that the form of the various osseous elements is well known. There is, however, some question as to the details of their articulation and their exact positions with relation to each other. The girdle of Cope, referred to above, was found with its elements in situ, but, as already mentioned, to a certain extent crushed and distorted out of shape. For example, the coracoids have been forced together on the median line, while the clavicles have buckled practically to a right angle and forced the interclavicle posteriorly, till it is overlapped by the coracoids. The clavicles also considerably overlap on the median line. Case considers this the normal position, but the evidence drawn from the uncrushed separate clavicles (A. M. N. H. No. 4307) above mentioned, would of itself necessitate a restoration such as that shown in figures 3, 10, and 15, when they are placed in relation to the scapulocoracoid of the same animal, of which a separate specimen has also been preserved. This is in the collections of the American Museum (A. M. N. H. 4307) and forms the basis of the restorations here figured. The mounted specimen in the American Museum has likewise been restored erroneously for the same reason (Fig. 1; cp. Fig. 7). The clavicles are bent inward until their extremities form a transverse line with each other and overlap, while the interclavicle is thrust backward like that in Cope's specimen.

This position appears to be quite unnatural and unnecessary. I believe that the conception here outlined (Figs. 3, 7, 10 and 15) presents not only a more natural contour and one that will admit of better muscular insertions and directions, as will be shown in a later section, but is in harmony with the conditions obtaining in *Archegosaurus*, *Mastodonosaurus*, *Lydekkerina* and other Permian amphibians in which



Fig. 5.—Shoulder girdle of *Archegosaurus* from ventral side, after von Meyer.

Note the correspondence with the restoration of the shoulder girdle of *Eryops* (Fig. 3). The clavicles are separated on the median line. In none of von Meyer's figures do they overlap. Note the position and arrangement of the ventral scutes.

these elements have either been preserved in their apparently correct relations, or show their method of articulation by their surface markings.

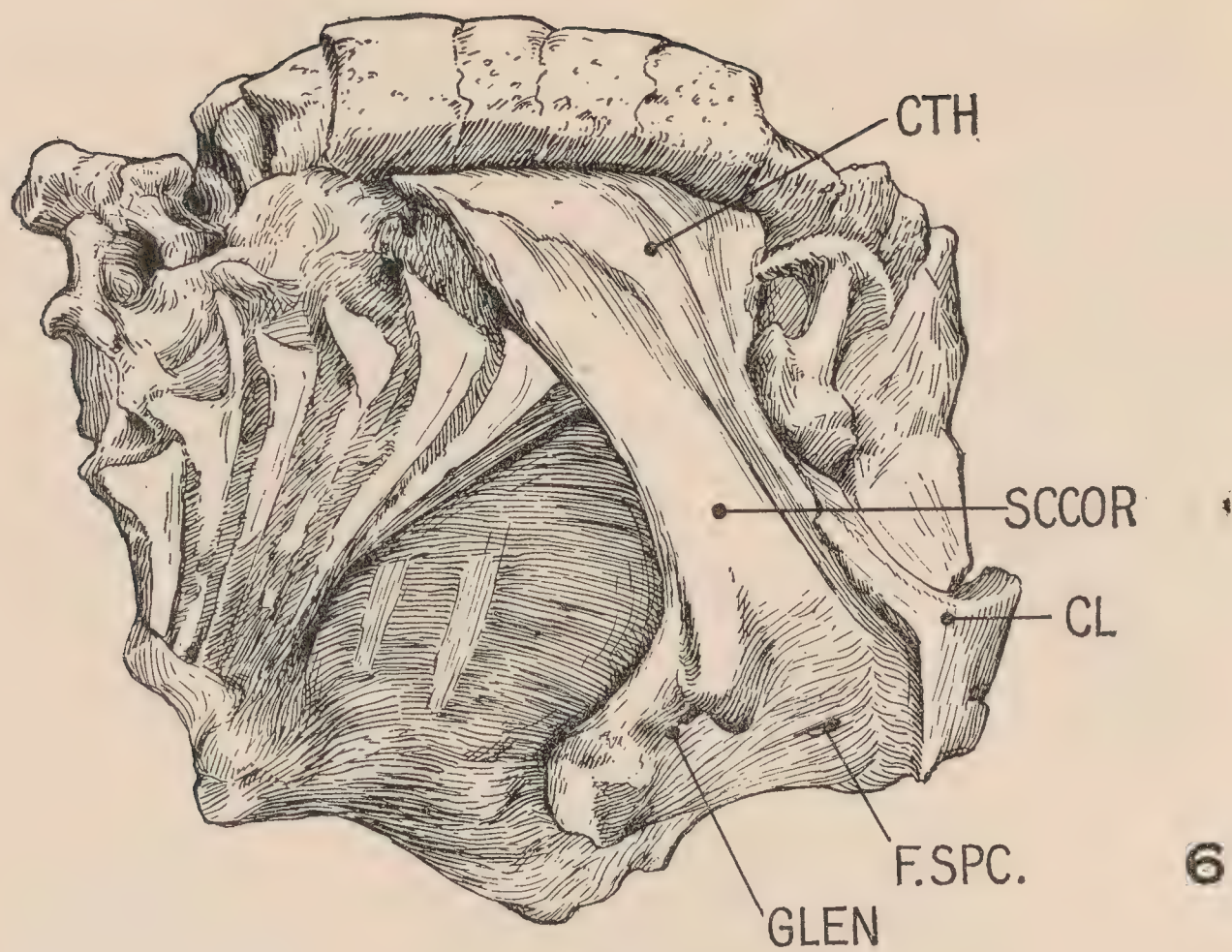
I am convinced that the lateral angles of the interclavicle were held between the ends of the clavicles, ventrally, and the cartilaginous portion of the coracoid, dorsally, as shown in figure 3, and that there was a considerable interval between the medial points of the two clavicles, thus leaving free the median more heavily sculptured ventral face of the interclavicle, together with its toothed anterior border. Indications on the inner surface of the clavicles seem to confirm this.

The articulation in *Archegosaurus* is especially well shown by von Meyer (1858, Pl. ix), from whose work a plate (Fig. 5) has been reproduced. Sketch figures in Watson's excellent article (1919, Fig. 9, p. 18, and Fig. 22, p. 37) also show the same conditions in *Mastodonsaurus* and *Lydekkerina*. All of these stegocephalians are closely related to *Eryops*, and show very clearly that the anterior edges of the rhomboid interclavicle were reserved for articulation with the ends of the clavicles, while the two posterior surfaces are in position to articulate with an anterior series of ventral scutes superficial to the cartilaginous border of the coracoid. In no cases do the clavicles overlap, though in *Metopias* (Fraas, 1888, Pl. xv), a relative of *Mastodonsaurus*, the girdle has been specialized to form a closely articulated plastronlike structure ventrally, with the medial edges of the clavicles meeting on the median line for a considerable distance, and apparently welded together, but nevertheless without overlapping. The posterior part of the "plastron" is formed by the interclavicle, the two anterior edges of which firmly interlock with the posteromedial edges of the clavicles.

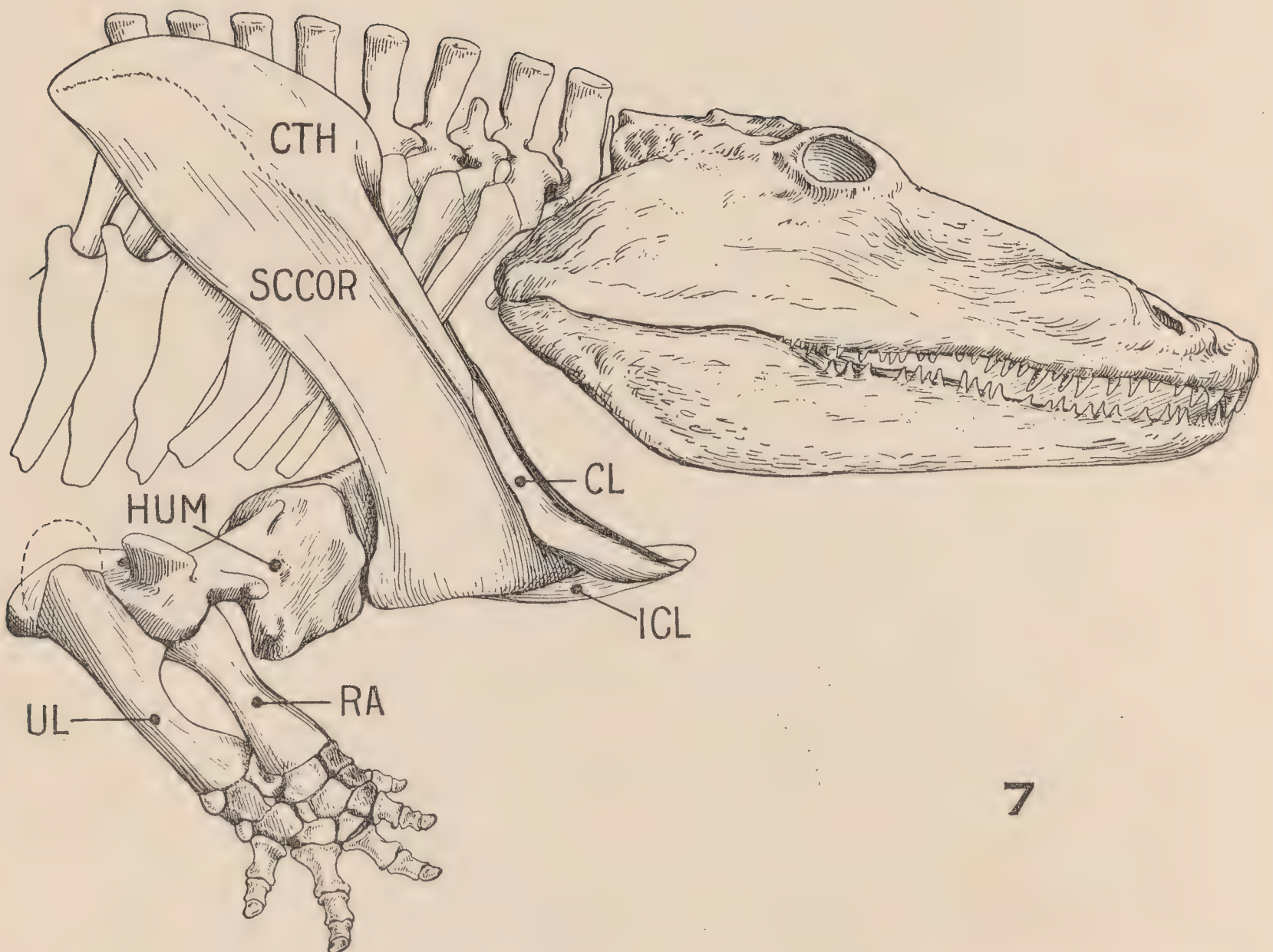
In the case of *Eryops* and *Archegosaurus*, these elements appear to have moved freely upon each other within certain limits, but I can see no indication that they normally overlapped, as shown in the mounted skeleton in the American Museum. It is also necessary to allow space for the coracoid cartilages indicated by the marginal grooves on the bone. They could not have been very wide and doubtless overlapped anteriorly, like the coracoids in modern urodele amphibians (*Megalobatrachus*, Fig. 12) and the precoracoids of *Sphenodon* (Fig. 14)¹. These cartilages doubtless slid freely one over the other and dorsal to the interclavicle, the lateral corners of which articulated in the notch formed by the ends of the clavicles and the anterior ends of the cartilaginous coracoids (precoracoids).² Shallow depressions on the dorsal or inner side of the fossil clavicles seem to confirm this method of articulation.

¹After Fürbringer (1900).

²The term "precoracoid" is taken to signify the anterior median portion of the coracoid cartilage in both reptiles and amphibians, while the "procoracoid" represents the dilated anterior projection of the coracoid in urodeles contiguous to the articulation with the scapula (see Figs. 12 and 14).



6

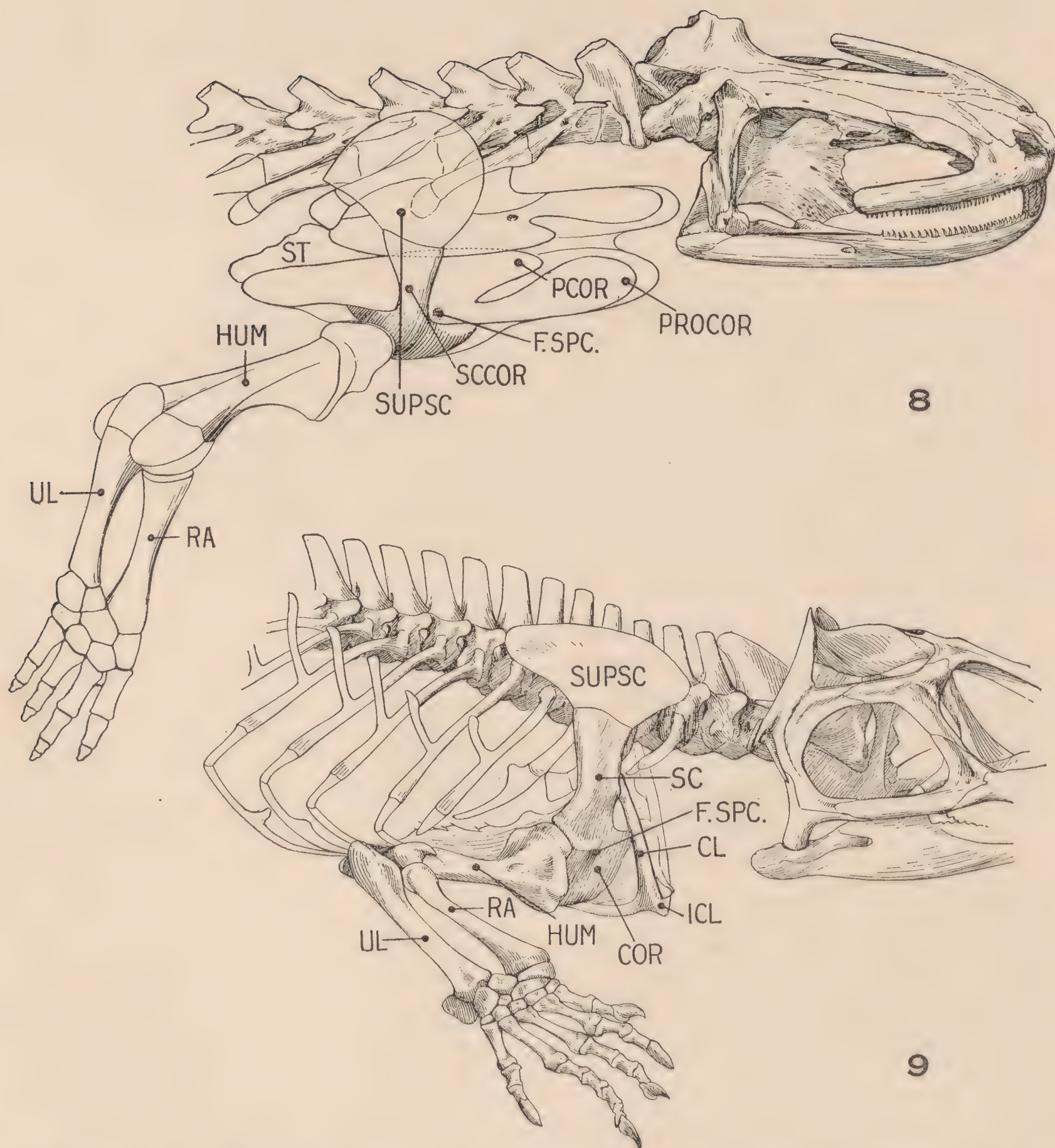


7

Fig. 6.—Original type of *Alegeinosaurus aphthitos* Case (A. M. N. H. No. 4756) drawn reversed for comparison with figure 7. See page 165.

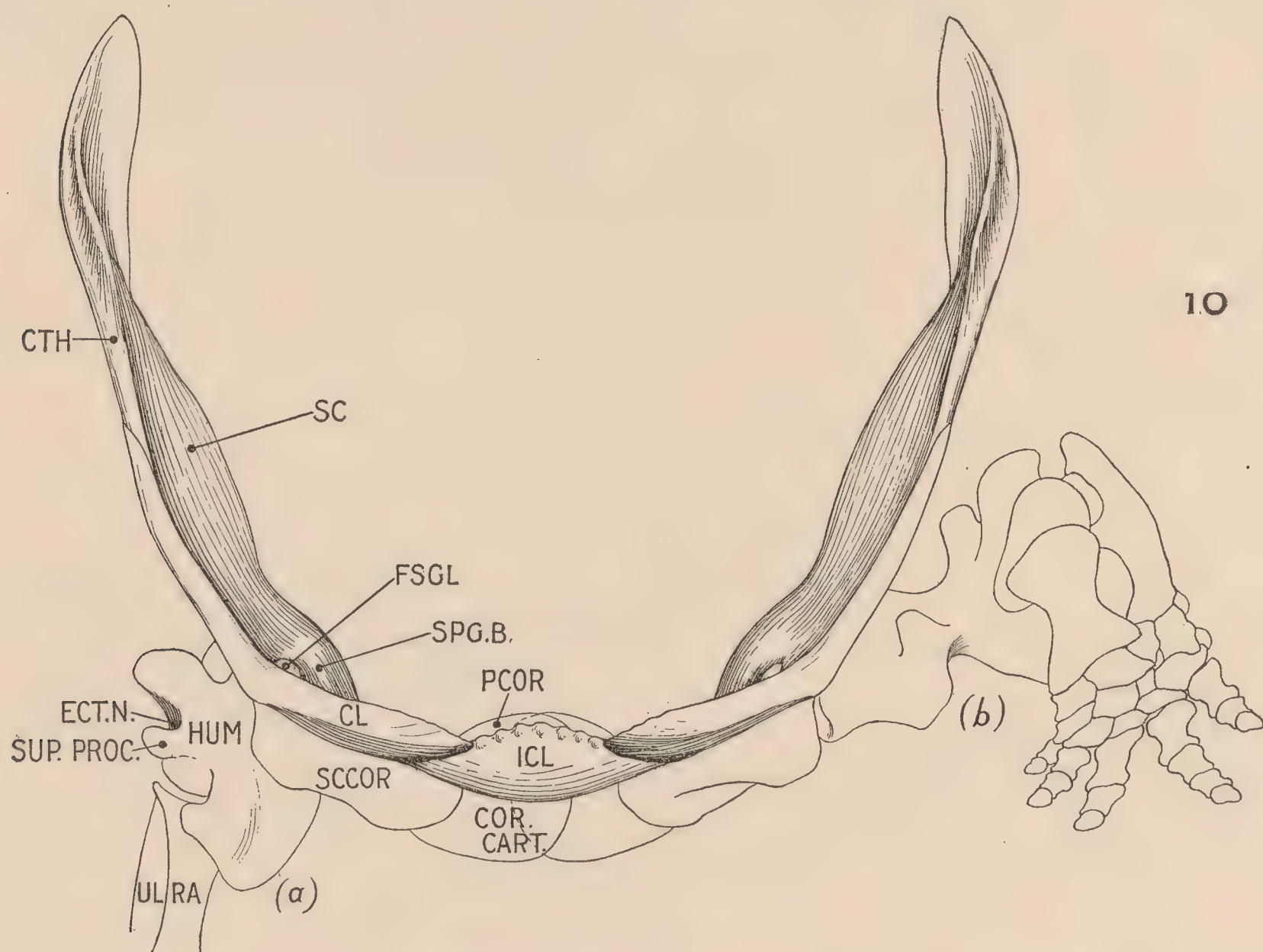
Fig. 7.—Restoration of shoulder girdle and pectoral limb of *Eryops*, shown from the right side.

Compare with present mounting of specimen in the American Museum (Fig. 1) and with figures 6 and 10. See pages 159-165.



Figs. 8, 9.—Shoulder girdle and fore limb of *Megalobatrachus maximus* and *Sphenodon punctatus* for comparison with *Eryops* (Fig. 7).

Again, the more anterior projection of the ventral part of the girdle on the median line, as compared with previous restorations, presents a more natural profile, and one more nearly in harmony with the elongate



Note relative positions of clavicles and interclavicle; the slope of the scapulæ; also the position of the humerus at the end of the stride (a), and at its beginning (b). The coracoid cartilage (COR. CART.) is inferred. See pages 158-159.

The natural dorsoventral slant of the scapulocoracoid is shown in the figure, and is obtained by this arrangement of the girdle when the ventral profile of the girdle is nearly parallel with the ground, and the dorsal extremity of the scapula with its cleithrum is properly oriented with reference to the spinal column. The suggested transverse slant of the scapulocoracoids is shown in figure 10, which brings the glenoid in the

best mechanical position with reference to the head of the humerus, where the supraglenoid buttresses it to the best advantage, and the glenoid itself partly arches over the condyle in such a manner that the weight of the animal is planted squarely upon it when the foot rests upon the ground. The outward swing of the scapula does not extend beyond a line drawn backward from the angle of the jaw, parallel to the vertebral column. The anteroposterior position of the scapulocoracoid harmonizes with that of the related form *Alegeinosaurus*, of which the Museum possesses a specimen (A. M. N. H. 4756) with the scapulocoracoid practically in situ (Fig. 6).

The hyoid apparatus, as may be seen by comparison with such a primitive living amphibian as *Megalobatrachus*, would fit nicely in the great triangular space embraced between the rami of the lower jaw and the anterior part of the shoulder girdle (Figs. 33a and 33c).

Articulation with the Humerus (Figs. 10 and 11).—The glenoid surface for articulation with the humerus is a “screw shaped” elongate excavation along an anteroposterior axis on the posterolateral face of the scapulocoracoid, immediately posterior to and beneath the supraglenoid buttress, and embraced by the backward extension of the latter and the “boss” or projecting process at the lower posterior angle of the scapula. As the shape of this surface can be well understood only by viewing it from different angles, a series of figures (Fig. 11 A to F) are given herewith to illustrate it, beginning with a directly lateral view (Fig. 11 A) and gradually rotating the bone, until it is seen from a directly posterior position (Fig. 11 F).

The articular surface of the condyle of the humerus is a counterpart of the glenoid in shape, and exactly fits into it, when the humerus is in its most posterior position. It is strap-shaped, the anterior half being situated on the extreme proximal end of the humerus head, and therefore directed forward when the humerus is in its posterior position and parallel with the body, as in figures 10 (a) and 15, while the posterior half of the condyle is mostly on the inner surface of the humerus head, curving forward spirally to become continuous with the anterior portion.

Thus, in the position above mentioned, the anterior part of the condyle fits against the portion of the glenoid situated against the back of the posteroventral process of the scapula (Fig. 11 A–F, x) while the medial portion of the condyle fits against the posterolateral portion of the glenoid (Fig. 11 A–F, y). The humerus is in this position when the animal has finished its stride and is on the point of raising its foot for the next. In reaching forward, the distal end of the humerus is moved

anteriorly, until the bone is practically at a right angle to the body, in the position shown in figure 10 (b). In this movement, the anterior part of the condyle, on the proximal end of the humerus head, slides backward through the glenoid, until it reaches the laterally directed posterior part (y), which, in the former position of the humerus, is articulated with the posterior part of the condyle. The latter has now slid back posterior to the glenoid.

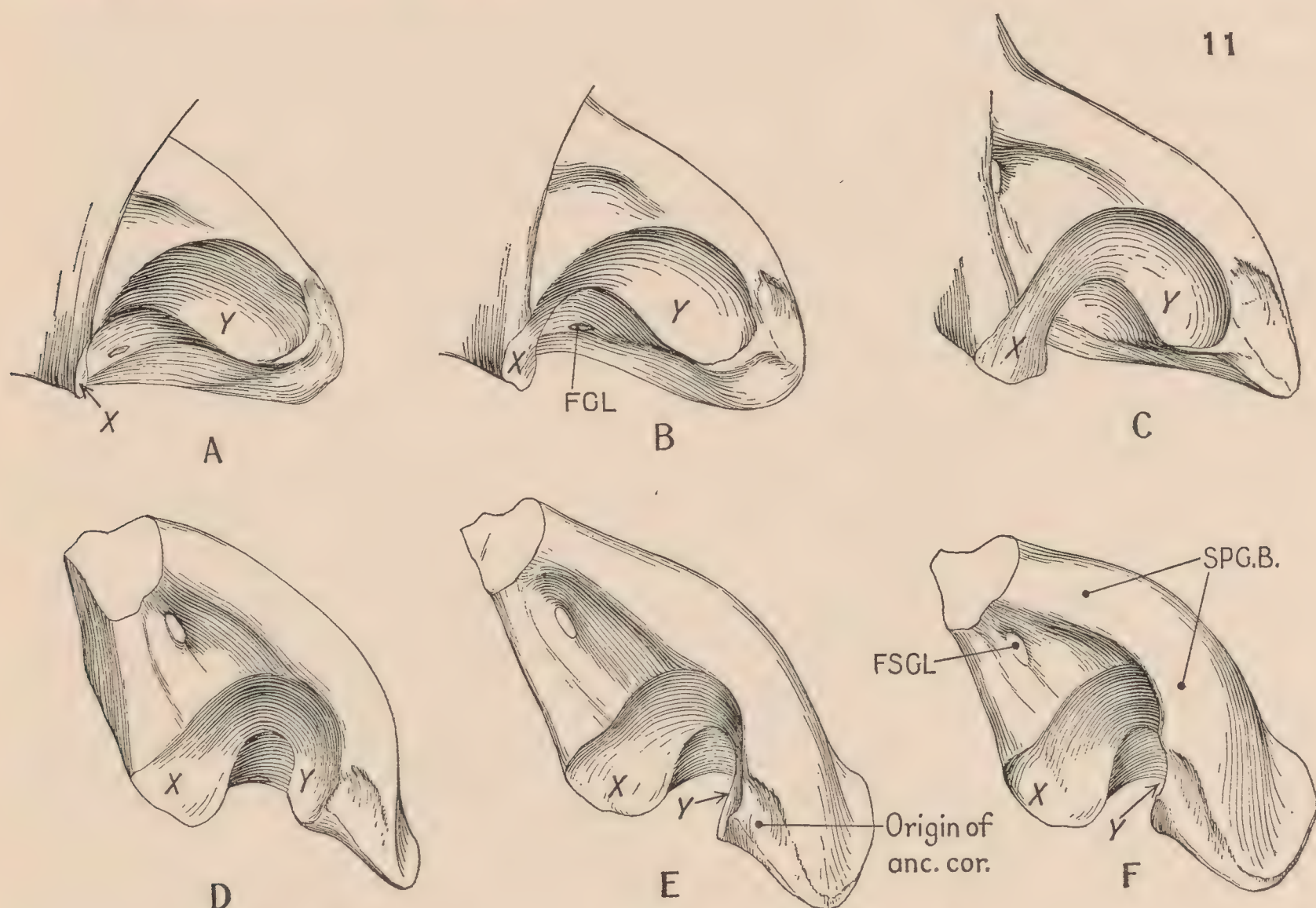


Fig. 11.—The screw-shaped glenoid cavity of *Eryops*.

As its peculiar shape can best be understood by viewing it from different angles, it is shown first at A as a directly lateral view. Then it is represented as gradually rotated in the successive views, B, C, D and E, and finally at F in a directly posterior position. When the humerus is in its most posterior position at the end of the stride, the anterior part of the screwshaped condyle, situated on the proximal end of the humerus head, fits at X, and the posterior part, which winds around to the medial side of the humerus head, snugly fits at Y, the entire condyle thus occupying the glenoid throughout its whole extent. When the humerus is moved forward in its reach at the beginning of the next stride, the condyle slides backward through the glenoid until the part formerly resting on X is half-way toward Y, and the posterior part of the condyle has moved out of the glenoid. Since the end of the humerus head now rests against that part of the glenoid formerly occupied by the side of the humerus head, the humerus has necessarily rotated on its longitudinal axis, in the meantime, through an angle of 90 degrees, as shown in figure 10.

Thus, the proximal end of the humerus head now fits in the part of the glenoid (y) formerly occupied by that part of the condyle which is on the inner side of the humerus head, and by this process the lower surface of the distal end of the humerus is turned upward about ninety degrees so that it now faces forward, at the same time that the limb is brought to a right angle with the body. This results from the screw shape of the

condyle and the fact that the end of the humerus head now fits in a part of the glenoid formerly occupied by the side of the head. In this position the lower limb would be raised and stretched forward. The weight of the body is now shifted over on to this limb, as the foot is brought down to the ground; the coracoid and clavicle together slide forward around the side of the interclavicle, and thus lengthen the forward reach of the limb.

The humerus cannot be thrust forward through more than a right angle without dislocation, but the articulation of the radius on the radial condyle of the humerus is very free, and the play of the scapulocoracoclavicular apparatus around the anterior border of the interclavicle, as well as the alternate shifting of the animal's weight first upon one side and then upon the other, with the resulting sinuous motion of the spine, produce a stride equivalent to a considerable forward thrust, and would probably enable the creature to bring its foot well under the body at the extreme forward limit of the stride.

Now the body is pulled forward, while the head of the humerus slides anteriorly through the glenoid, until the condyle occupies its first position, and, at the completion of the stride, the limb is again parallel with the body, with the elbow directed posteriorly. Then with a thrust upward on the toes, the weight of the body is thrown over to the opposite side, when the process is repeated.

Watson says (1917a, p. 3) that the screw-shaped glenoid and the articular condyle "wound around the head of the humerus" of *Eryops* "show that the humerus has its motions very strictly limited; it is incapable of any rotation on its long axis, and that axis must be so placed that it lies nearly parallel to the ground," and that "its only possible motion is such that a point on the distal extremity when viewed directly laterally moves along a small segment of a large circle placed parallel to the animal's sagittal plane, with the chord of the segment placed nearly horizontally; in other words, as the humerus moves forward its outer end is first slightly depressed and then raised again."

However, by means of specimens in the American Museum, I am able to demonstrate the possibility of a motion such as I have just described, and to show that a strap-shaped condyle which winds about the humerus head so as to fit into a screw-shaped glenoid, would necessarily give the humerus a virtual rotation on its long axis, which in this case would amount to about ninety degrees.

It may be objected that this motion would cause the posterior part of the condyle to pass outside the limits of the glenoid posteriorly in the

forward motion of the humerus. The obvious answer is, that this is true of the condyles of modern amphibians, reptiles and mammals to an even greater extent, for the articular surface of the condyle is usually much larger than that of the glenoid, so that portions of its surface are continually passing away from the area of contact with the glenoid, the humerus being held in joint only by the walls of the articular capsule.

Doubtless *Eryops* had such a capsule, and there was sufficient play to allow half the surface of the condyle to pass posteriorly to the glenoid.

The very complete ossification of the appendicular skeleton would show that the cartilaginous caps of the joints were comparatively thin.

b. The Shoulder Girdle of *Megalobatrachus*

General Description.—The shoulder girdle of *Megalobatrachus* (Fig. 12) is largely a cartilaginous structure, its only ossified portion being the bony scapula. This is a somewhat flattened cylinder of bone rising vertically at the side of the body, expanding to a moderate degree dorsally to articulate with the cartilaginous suprascapula, and having a larger fan-shaped expansion ventrally which articulates with the extensive coracoid cartilage. By far the greater part of this ventral expansion is directed anteriorly toward the procoracoid, while the smaller posterior portion is included within the anterior part of the glenoid. At about the center of the ventral expansion, the bone is pierced by a foramen (Figs. 13a and 13b, FGL?) which seems to be homologous with the glenoid foramen of *Eryops*. A small blood-vessel, apparently a branch of the A. circumflexa scapulæ, passes through this opening and connects on the dorsal side of the coracoid with A. supracoracoidea by means of an anastomosing branch. Dorsolaterally from this foramen is a shallow pit (FSGL?), the cavity of which is directed posteriorly toward the glenoid border of the scapulocoracoid but does not pierce it in the specimen examined. This blind pit is so situated as to suggest that it is the remnant of a former supraglenoid foramen, while the bridge of bone arching its opening posteriorly and forming the posterior border of the scapulocoracoid strongly resembles the supraglenoid buttress of *Eryops*, but in a greatly reduced condition. It leads directly to that portion of the scapulocoracoid which embraces the anterior part of the glenoid cavity, and which is associated with the M. subscapularis, as in *Eryops*.

This provisional interpretation would indicate that the mesocoracoid arch of fishes, which as suggested by Romer (1922) may have given rise to the supraglenoid buttress of stegocephalians and primitive reptiles, and, through the latter, to the ligamentum sternoscapulare internum of

Sphenodon and modern lizards, is also ancestral through the stegocephs on another line of evolution to this buttresslike remnant surviving in *Megalobatrachus*. It would be interesting to note whether this is a unique case, or if a similar structure occurs in other urodeles.

If the above mentioned homologies are correct, the supracoracoid foramen in *Megalobatrachus* has been carried medially and posteriorly, as compared with *Eryops*, in correlation with the expansive evolution of the cartilaginous part of the coracoid.

Suprascapula.—The suprascapula is a thin, disklike expansion of cartilage surmounting the bony scapula. Its anterior edge thins out into a band of connective tissue which embraces and unites with the levator scapulæ muscle. Posteriorly, it shades insensibly to a thin band of connective tissue, continuous posteroventrally with the enveloping connective sheath of the body.

Coracoid.—The coracoid cartilage comprises two portions, the coracoid proper and the procoracoid.

The coracoid proper is a fan-shaped expansion of cartilage, relatively narrow at its lateral junction with the procoracoid and the scapula and with a broadly rounded margin medially. This medial margin overlaps the coracoid of the other side, the right coracoid being the more ventral one.

Procoracoid.—The procoracoid (Fig. 12) is a thin, elongate, spatulate cartilage extending forward from its junction with the coracoid and scapula on the ventrolateral margin of the body, superficial to the trunk musculature. Its anterior limit is an imaginary line drawn between the posterior angles of the jaw. Its medial margin bounds an indentation embraced between it and the coracoid proper, extending almost to the ventral edge of the scapula. This indentation is filled by a thin membrane which is continued anteriorly around the forward end of the procoracoid. Near the junction of the coracoid with the procoracoid, the cartilage is pierced by the supracoracoid foramen.

Sternum.—The sternum (Fig. 12) is a single triangular piece of thin cartilage with a shallow posterior median indentation, causing it to appear somewhat heart-shaped. It occupies the median angle formed by the posterointernal margins of the overlapping coracoids, which movably articulate with it by means of pocketlike slots or grooves, situated on the dorsal side of its anterior borders.

Homologies of the Amphibian Shoulder Girdle.—The preponderance of cartilage, or rather the failure to ossify, in the greater part of the shoulder girdle of *Megalobatrachus*, while an adaptation to aquatic life,

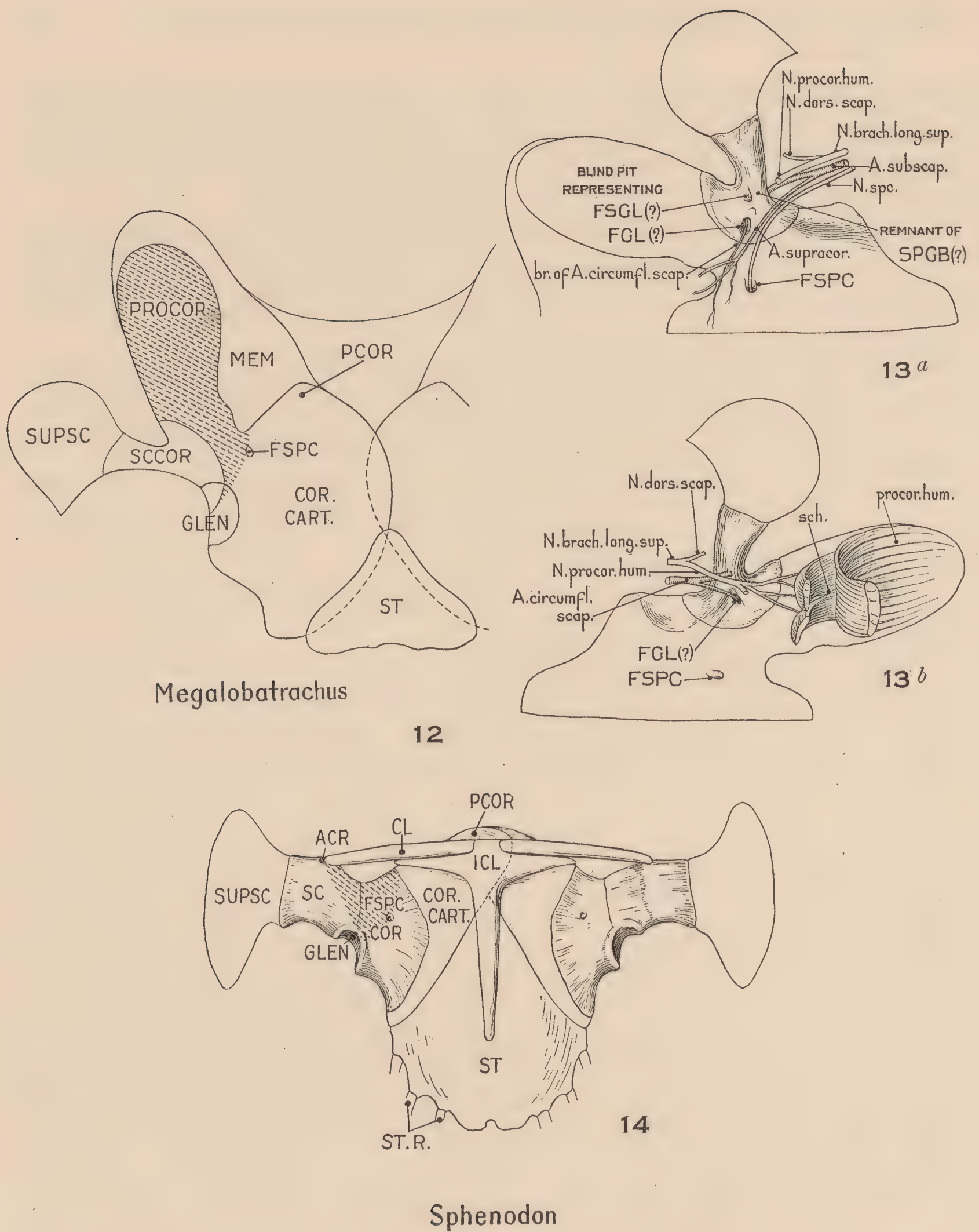


Fig. 12.—The shoulder girdle of *Megalobatrachus* shown from the ventral side for comparison with figures 3 and 14 (represented in one plane).

Figs. 13a and 13b.—The scapulocoracoid and procoracoid of *Megalobatrachus* from the inner (13a) and outer (13b) side, to show the probable remnant of the supra-glenoid buttress (SPG.B) of stegocephs; the blind pit (FSG) probably representing the supra-glenoid fossa; the homologue (?) of the glenoid foramen (FGL), and the distribution of nerves and bloodvessels in this region. In 13b, the relation of the *M. scapulohumeralis* (sch.) to *M. procoracohumeralis* (procor. hum.) is also shown.

Fig. 14.—The shoulder girdle of *Sphenodon* shown from the ventral side for comparison with figures 3 and 12 (represented in one plane, adapted from Fürbringer).

The shaded areas in this figure and in Fig. 12 represent areas considered homologous in this paper.

is also an inheritance of great antiquity. The urodeles according to Moodie (1916) probably date back to Carboniferous times, when, this author asserts, they form a direct ancestral connection with the aquatic branchiosaurs, through such forms as *Micrerpeton caudatum* Moodie. The branchiosaur girdle was largely cartilaginous with a single center of ossification, the "coracoid" of authors. This bone, however, is certainly a scapula, or at least a scapulocoracoid, since the element often referred to as the "scapula" has the form and position of the cleithrum, articulating in the conventional way with the clavicles, and situated anterodorsally to the bone in question, which should therefore be termed the scapulocoracoid ossification (See Gegenbaur, 1895). This view is confirmed by the fact that the element is usually associated with the humerus head, as seen in the fossils of *Archegosaurus* where they are preserved nearly in situ (Fig. 5), and apparently first ossified to mechanically reinforce the shoulder joint. It is evident from the relative positions of the bones as preserved in many cases, that the remainder of the girdle was largely of cartilage.

In aquatic groups the ossification area would remain relatively small, while in terrestrial, or heavy-bodied, semiterrestrial forms, like *Eryops*, it would be greatly strengthened, accounting for the very complete ossification of the latter form. Throughout the urodeles, the scapula alone is ossified. Forms like *Proteus*, *Necturus* and the young axolotl have the narrow scapular stem alone ossified. Others, such as *Megalobatrachus*, show that the bony area invades the anterior border of the glenoid. In *Molge*, it embraces not only a large part of the glenoid, but the proximal part of the procoracoid as well, and also includes a small part of the coracoid, completely surrounding the supracoracoid foramen, all from a single center of ossification. In the adult *Amblystoma*, the single ossification is even more extensive, including the entire glenoid, with a considerable invasion of the coracoid. In all these cases the cartilaginous area is very extensive, but the ossified portion appears to be a true scapulocoracoid bone, like that of *Eryops*, but without such an extensive invasion of the coracoidal area and indicating that this is an amphibian character inherited from the very earliest times, before the origin of the reptilian stock.¹

The fossil remains of the branchiosaurs are comparable to the condition in urodeles, except that the former still possess the dermal cleithrum, clavicle and interclavicle, which have been lost by the latter through a continuance down the ages of the aquatic habit of life. This

¹*Siren*, however, and perhaps others are exceptions to this general rule.

loss seems to be the result of a progressively general failure of the dermal skeleton to develop in the urodele stem, since they have also completely lost the external dermal skeleton of bony scales and scutes characteristic of the branchiosaurs. The Carboniferous amphibians, in general, including branchiosaurs, microsaur and stegocephalians, were well equipped with dermal armature, at least on the ventral side. In the modern urodeles, the only derm-bones remaining are those of the skull, and even here they are greatly reduced in number. Hence, this reduction of the exoskeleton must be regarded as one of the great features of urodele history from the earliest times, and indicates that long-continued adaptation to aquatic life, in this case, affects first of all the dermal skeleton, the only ossifications remaining in the appendicular apparatus being of cartilaginous origin.

The case is different in the Anura. Here the terrestrial leaping habit has necessitated the retention of a compact, well-strengthened pectoral girdle as well as the pelvic specialization along this line.¹ Not only the scapula but also the coracoid elements are well ossified, while a dermal clavicle has been retained to overlies and strengthen the "procoracoid." Even the suprascapula possesses a superficial ossification, and Schmalhausen (1917) has shown, from embryological data, that this is a dermal ossification, corresponding closely in position and development with the dermal cleithrum, and is without doubt a survival of this ancient structure. Otherwise, the dermal skeleton has also been lost in the girdle of the Anura, but these traces seem to speak for an antiquity of the group extending back to a much earlier time than the Jurassic, from which the earliest unquestioned fossils have hitherto been taken, and adding interest to the suggestion (Moodie, 1916, p. 73) that the Carboniferous *Pelion lyelli* Wyman, with its strong, frog-like characters, may be an anuran or at least transitional to this stock.²

The girdle of Anura articulates with a well-developed and partly ossified cartilaginous sternal apparatus on the median ventral line of the body, which has no trace of dermal elements. The "procoracoid" of authors, an anterior transverse bar of cartilage, underlies and is reinforced by a "clavicle" which appears to be of membrane bone.³ The "obturator fossa" separates this from the coracoid proper, and through it passes the supracoracoid nerve. Authors generally have homologized the anterior element with the procoracoid of urodeles, the "obturator

¹Though the hind limbs may be the principal factor in the act of leaping (Holmes, 1907, p. 27), the shock of landing is partly absorbed by the fore-limbs and the pectoral girdle with their musculature.

²Gregory (1917) has brought forward good evidence, however, to show that the Anura may have been derived structurally directly from the rhachitomous stegocephalians.

³Gegenbaur, C. 1897. "Clavicula and Cleithrum," Morphol. Jahrb., XXIII.

fossa" with the coracoprocoracoid fenestra of the latter, and the posterior element as the coracoid in both groups. Anthony and Vallois (1914), however, though they accept the homology of the coracoid, regard the "procoracoid" of Anura as not a true procoracoid, but merely a coracoidal prolongation, and the anuran acromion as homologous with the procoracoid of urodeles. They consider the "obturator fossa," therefore, as an enlarged space about the supracoracoid nerve, and hence, as it were, a supracoracoid fossa. The homologue of the coracoprocoracoid fenestra of urodeles would then be represented by the shallow indentation of the anterior border of the girdle, between the acromion and the "soi-disant procoracoïde" of anurans. They base their argument on the following points:

(1) The acromion of anurans is directed cranially like the procoracoid of urodeles.

(2) The axis of the glenoid is directed toward the coracoprocoracoid fenestra in urodeles and toward the indentation between the acromion and so-called "procoracoid" of anurans.

(3) The supracoracoid nerve passes through a supracoracoid foramen in the coracoid cartilage in urodeles and through the "obturator fossa" in anurans.

(4) The acromiohumeral muscle of anurans corresponds in form, mode of insertion, function and double innervation (by N. dorsalis scapulæ and N. supracoracoideus) to the procoracohumeralis of urodeles.

(5) This interpretation simplifies the otherwise puzzling homology of the musculature in general of the pectoral girdle in the two groups.

In my opinion the points of Anthony and Vallois have been, as a whole, well taken. In addition I would call attention to the adaptive changes the various parts of the girdle pass through, while the course of the supracoracoid nerve remains relatively stable with reference to the main topography of the girdle. Even in Anura it remains in a position corresponding to that in urodeles, though the axis of the glenoid has changed in its direction, the procoracoid is reduced to an acromion, and the supracoracoid foramen has enlarged to an "obturator fossa."

The figures of Anthony and Vallois also illustrate the variability of the ossification of the scapulocoracoid in urodeles. In *Siren* and *Menobranchus* (*Necturus*) the scapular shaft only is ossified; in *Cryptobranchus* (*Megalobatrachus*) the ossification has invaded the coracoid and the anterior border of the glenoid; in *Triton* (*Molge*) it includes the supracoracoid foramen and the coracoid as far as the coracoprocoracoid fenestra, as well as the greater part of the glenoid. This same process is shown

in the ontogeny of the axolotl larva (*Amblystoma*), in young specimens of which only the shaft of the scapula is ossified, while older examples show that the ossification includes a large portion of the coracoid as well, including the entire glenoid and the supracoracoid foramen.

Through all, the general position of the supracoracoid foramen seems relatively stationary, and would seem to be a landmark of importance, ranking with the acromion in this respect, and aiding in identifying the precoracoidal part of the girdle. The urodele condition corresponds to that in *Eryops*, where the scapulocoracoid bone has grown around the supracoracoid foramen.

This condition is, therefore, another amphibian character of great antiquity. The part of the *Eryops* coracoidal area anterior to the supracoracoid foramen may be conceived as homologous with the proximal part of the precoracoidal area of urodeles. It will be noted that the precoracoidal region of *Eryops* includes the greater part if not all the ossified part of the coracoidal expanse, while the metacoracoid is either very small and not separated by a suture or does not exist in *Eryops*.

c. The Shoulder Girdle of *Sphenodon*

General Description and Comparison with Megalobatrachus and Sphenodon.—The girdle is figured for comparison (Fig. 14¹). The principal differences, as compared with the amphibian girdle, are correlated with a much more efficient adaptation for an active terrestrial life. There is an ossified scapula and suprascapula, and the coracoid is separated from the scapula by a suture on the line of the glenoid and shares the glenoid cavity with it. The bony coracoid is pierced by a supracoracoid foramen, anterior to which the precoracoidal portion is bony proximally, and is continued forward by a cartilaginous precoracoidal area, overlapping that of the other side, just dorsal to the interclavicle and projecting slightly beyond it anteriorly. Posteromedially, the coracoidal cartilage is continuous with the cartilaginous extension of the coracoid proper. There is a dermal clavicle connecting the scapula with the interclavicle, articulating with the former by means of an acromion, and with the latter on the ventral side, a short distance from the median line of the interclavicle. It therefore does not overlap its fellow on the opposite side.

The interclavicle (the episternum of Fürbringer) is T-shaped and widely expanded anteriorly to form a well-braced structure with the clavicles, and extends posteriorly along the median line to unite with the sternum.

¹Reproduced from Fürbringer (1900).

Posteromedially the cartilaginous portions of the coracoid articulate movably in a marginal groove with the sternum, which is much stronger and larger, and of more significance to the girdle than in *Megalobatrachus*. The posterior border articulates with three pairs of sternal ribs.

The whole apparatus forms an efficient structure of support for the internal organs, and for the attachment of the powerful ventral muscles inserting on the proximal part of the limb and supporting the weight of the body.

The following differences, as compared with the pectoral girdle of *Megalobatrachus*, are especially to be noted:

- (1) More extensive ossification,
- (2) Ossification of scapula and coracoid from two centers,
- (3) Presence of dermal clavicle,
- (4) Presence of interclavicle,
- (5) Larger and stronger sternum articulating with ventral ribs.

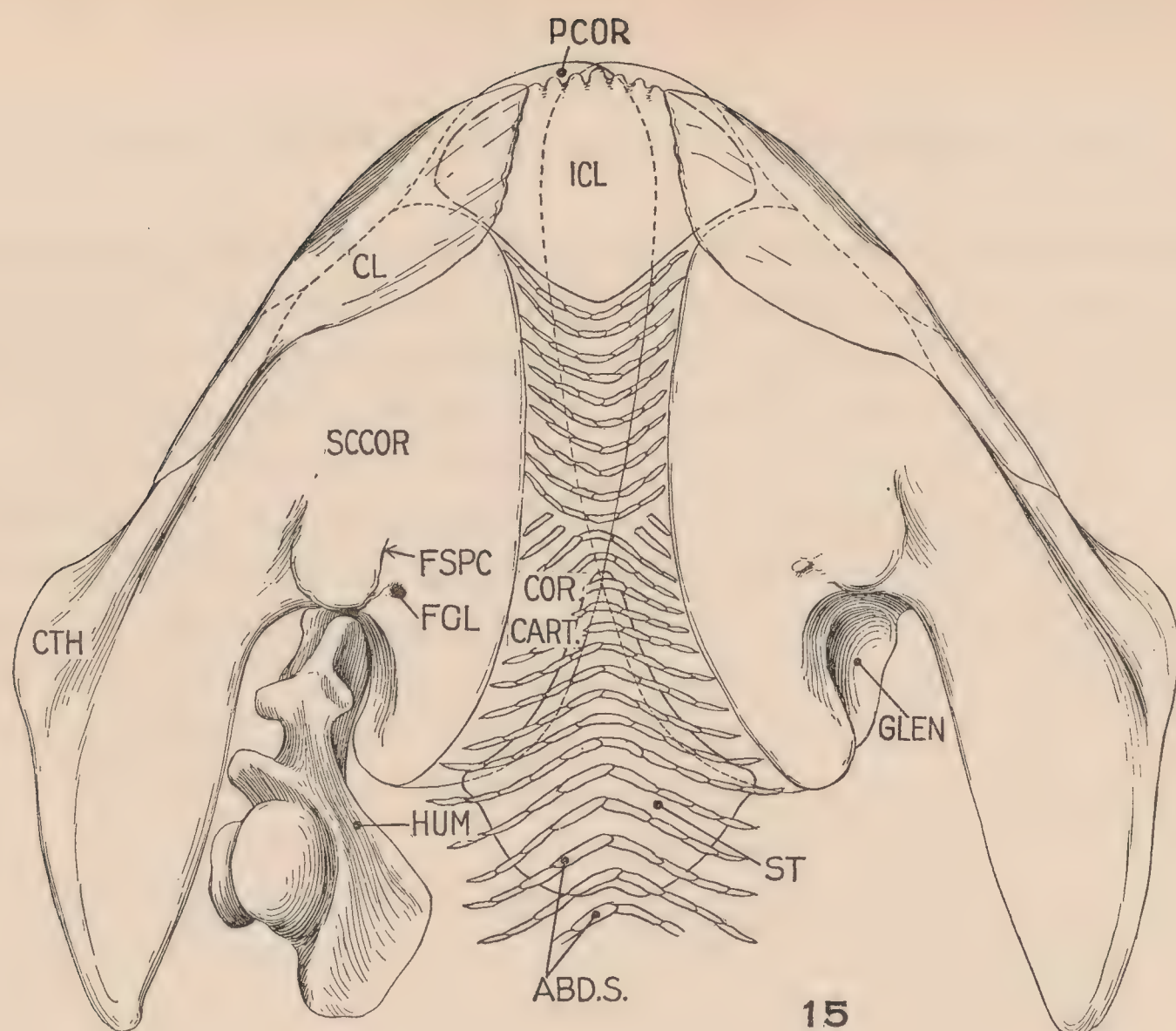
The principal differences as compared with the girdle of *Eryops* are:

- (1) Absence of cleithrum,
- (2) Ossification of scapula and coracoid, from two centers instead of one,
- (3) Posterior median extension of interclavicle.

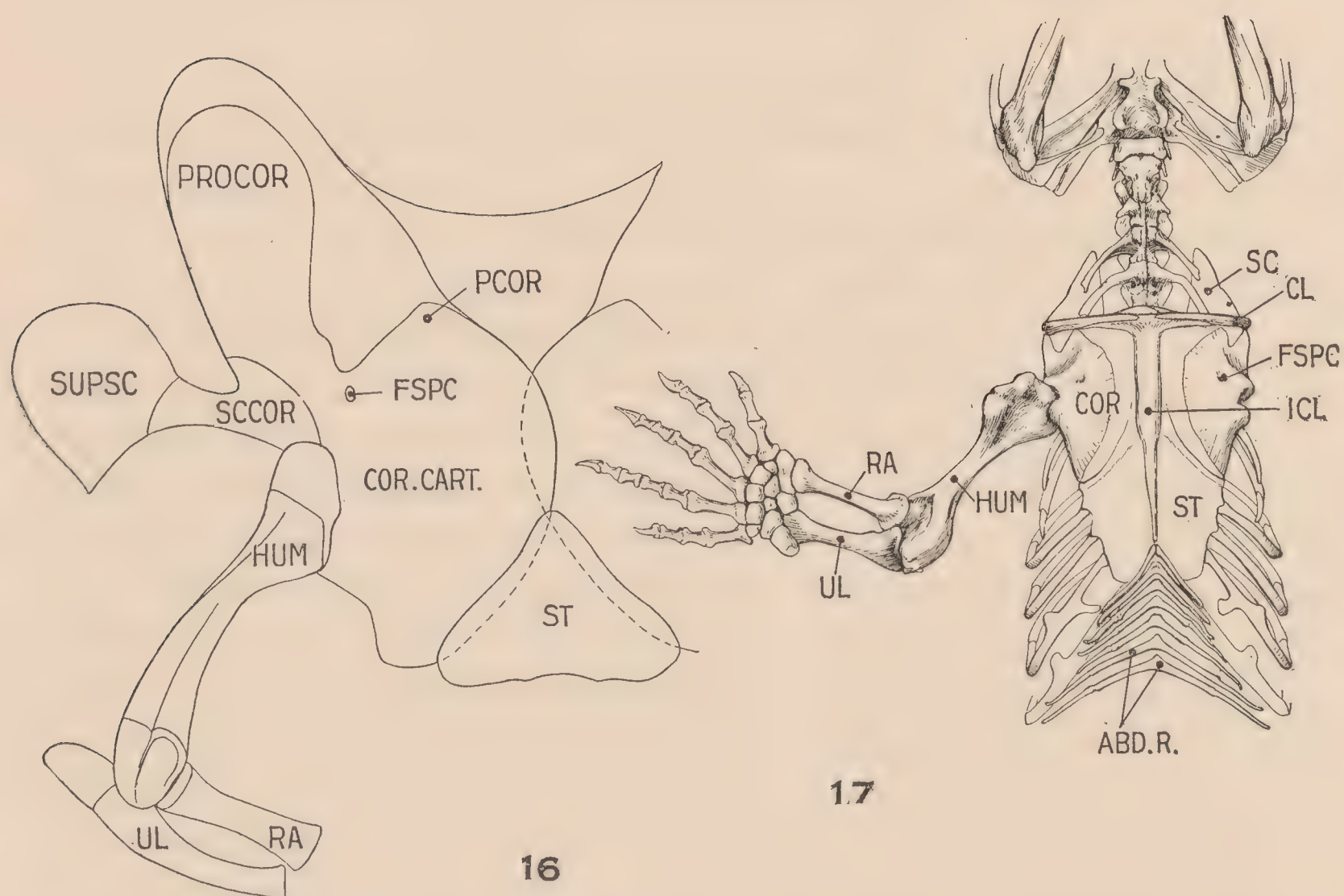
d. General Homologies of the Pectoral Girdle of *Eryops*,
Megalobatrachus and *Sphenodon*

General Conditions of the Homology.—The position of *Eryops*, as a member of the ancestral group, Stegocephalia, should render it possible to derive from the elements of its girdle those of the reptiles on the one hand, as typified by the generalized reptile, *Sphenodon*, and those of the urodele amphibians, on the other, as exemplified by *Megalobatrachus*; for it is generally admitted that the reptiles are an offshoot of the earliest Stegocephalia through the cotylosaurs, while the urodeles are derived from other stocks of the same basal group. Likewise, a comparison of the skeletons of these two recent forms with those of Permian and Carboniferous times, should help to throw light on the unknown cartilaginous portions of the *Eryops* skeleton, and of its method of articulation.

It must be borne in mind that the original skeleton of all osseous vertebrates is laid down in cartilage derived from membranous areas of mesenchyme. Therefore the real homologous regions are to be sought in the basic cartilage, ossified to a greater or less degree due to mechanical



15



17

16

Fig. 15.—The shoulder girdle and right humerus of *Eryops*, restored, and shown from the ventral side, in perspective, to illustrate the inferred cartilaginous epicoracoids (COR. CART.), and sternum (ST), and their relations to the underlying abdominal scutes (ABD.S.). Compare with Figs. 16 and 17.

Figs. 16 and 17.—Ventral view of pectoral girdles of *Megalobatrachus* and *Sphenodon* for comparison with Fig. 15.

Note the total lack of dermal elements in *Megalobatrachus* (Fig. 16), and their retention in *Sphenodon* (Fig. 17).

stresses or hereditary tendencies, and to which has been applied a certain number of membrane bones derived originally from dermal scutes of the original superficial bony armature.

The mechanical stresses increase the size of the cartilage bones and preserve the ancestral quota of dermal bones in a more or less expanded condition.

Conversely, aquatic habitat, providing, as it does, an evenly distributed external support for the body, may considerably diminish the mechanical stresses on the skeleton and tend to retard the development of ossified areas and to cause the loss of dermal ossifications.

The ancient branchiosaurs had already started on the road toward the series of aquatic specializations evident in modern urodeles, while *Eryops* and the related stegocephs had begun the adaptations leading to terrestrial life further evolved successively by Permian cotylosaurs and the other groups of fossil reptiles, and brought down to recent times by the specializations of modern reptiles, birds and mammals, with *Sphenodon* as a connecting link with the past.

Homology of the Suprascapula.—The cartilaginous suprascapula is obviously homologous in both *Sphenodon* and *Megalobatrachus*. It is easily recognizable in all urodeles and reptiles, though in varying degrees of extension. In Anura, the cartilage is more or less covered by a dermal ossification, which (Schmalhausen, 1917) appears in the embryo as a bladelike plate overlying the anterior edge of the suprascapula and, in the adult, extends over the proximal part of that cartilage, retaining, however, a tendency to a greater expansion on the anterior edge. It seems quite clear from the researches of Schmalhausen that this membrane bone is a rudimentary cleithrum. This strengthens the view that the cleithrum in *Eryops*, and in all primitive tetrapods, capping as it does the dorsal end of the scapular blade, and extending beyond it dorsally and anteriorly, was laid down over a cartilaginous base which was the dorsal unossified end of the scapula, homologous with the later suprascapula. It is also possible that the distal portion of the scapular blade itself extended its ossification somewhat over that part of the general primitive cartilaginous shoulder girdle corresponding to the suprascapula in later amphibians and reptiles.

Homology of the Scapula.—In *Eryops* and other Carboniferous and Permian Amphibia, the scapular blade, as stated previously, forms but a part of the same ossification that includes the ossified portion of the coracoid, and thus forms with it a single bone, the scapulocoracoid. This ossification may also include, dorsally, the proximal part of the later

cartilaginous suprascapula, as just stated in connection with the discussion of that element. In *Sphenodon*, the term scapula is applied only to the dorsal ossification above the glenoid, which is separated from the coracoid by a suture passing through and anterior to the glenoid cavity itself. In later reptile groups the scapula is similarly limited. Dorsally, it unites with the cartilaginous suprascapula.

Among the urodeles, the scapula of authors should more properly be termed a scapulocoracoid, in so far as it is a single ossification, which includes a varying amount of the proximal part of the coracoidal and procoracoidal surfaces and occasionally surrounds the supracoracoid foramen (page 173). In this group, therefore, it is very nearly homologous with the scapulocoracoid of *Eryops*, while the cartilaginous surface in which the ossification took place is nearly homologous with the cartilage invaded by the double ossification of *Sphenodon* and the Permian reptiles.

The anurans show a condition in which the scapula is nearly homologous with that of reptiles, having an ossification separated by a suture from the coracoid in the region of the glenoid cavity.

Homology of the Coracoid and Procoracoid.—The coracoidal portion of the stegocephalian scapulocoracoid, exemplified by *Eryops*, as previously mentioned, possesses a marginal groove on its median edge which betrays the existence of a cartilaginous extension of the girdle, as indicated in figure 15. Its medial extent can only be surmised, but if the two halves of the girdle be articulated as in the figure, and the conditions compared with those in *Archegosaurus* (Fig. 5), it is evident that it must have been relatively narrow, but of wider extent anteriorly, to form a precoracoidal expansion similar to that of *Sphenodon*. Apparently *Sphenodon* is primitive in this respect. Hence in figure 15, the restoration of the cartilage is adapted from that in the latter type. The shoulder girdle of modern urodeles in general is secondarily adapted to aquatic life, both in its failure to ossify in by far its greater expanse and in the fact that a procoracoidal region¹ has become extensively developed

¹The following table indicates the homologies of the scapula and coracoid here adopted, including those of the procoracoid and precoracoid:—

AMPHIBIA	ANCESTRAL AMPHIBIA	REPTILIA
Suprascapula	CORACOSCAPULA {	Pars suprascapularis
Scapulocoracoid <i>pars</i> (vertical stem)		Pars scapularis s.s.
Pars glenoidea		Pars glenoidea
Procoracoid (a distinct process in urodeles) = "acromion" of Anura		"Procoracoid" of chelonians and plesiosaurs
Scapulocoracoid <i>pars</i> (ventral body expansion) + Cartilaginous coracoid		Precoracoid (epicoracoid) Coracoid (metacoracoid)

laterally to lie along the ventrolateral margin of the body in response to the general flattening and broadening of the ventral surface of the body, as an aquatic adaptation. This is well exemplified in *Megalobatrachus* (Fig. 16), where the effect is seen on the anterior border of the ossified scapulocoracoid as well, which is strongly concave where the ossification includes the proximal part of the procoracoidal expansion. A similar condition is evident in *Molge* and the adult *Amblystoma*, but in forms like the young of the latter, where the ossification has not proceeded so far, and in *Proteus*, *Siren* and *Necturus*, where only the vertical stem is ever ossified and no part of the procoracoid is included, the anterior edge of the scapula is practically straight. In urodeles, the cartilaginous procoracoid is very variable, extending far forward in *Megalobatrachus* and *Necturus*, and remaining comparatively undeveloped in comparison with the coracoid in *Molge* and the larval *Amblystoma*, while in the adult of the latter it becomes entirely united and continuous with the coracoid, except for a small fenestra.

The coracoid proper in modern urodeles is an expanded oval structure of considerable extent, in correlation with the broad, flattened under surface of the body. In some forms, it is entirely cartilaginous; in others, as above stated, it is invaded proximally by the ventral portion of the scapulocoracoid ossification. In general, a broad, thin plate of cartilage is developed in correlation with the expansion of muscular attachments made necessary by the disappearance of dermal clavicle, interclavicle and other advantageously located and braced areas of muscular purchase. As will be shown later, muscles attached to the clavicle and the anterior coracoidal margin in reptiles are attached only to the elongate procoracoid in urodeles, while the more greatly expanded procoracoid in the latter compensates for the loss of the clavicle possessed by the former.

The precoracoid of *Eryops* was doubtless continuous with the coracoid and directed somewhat toward the median line, as in the case of *Sphenodon*, since its girdle with its clavicle and interclavicle is arranged similarly, and it was unaffected by aquatic adaptations, as in urodeles. The position of the girdle as restored would permit an extension of a precoracoid anteriorly somewhat beyond the clavicles, as shown in the figure.

Homology of the Clavicles.—The clavicle in *Eryops* is clearly homologous with that of *Sphenodon*. It articulates with the scapula in a similar way, except that the latter, in reptiles, possesses an acromion. It doubtless formed the attachment for the deltoid posteriorly, and for

the trapezius anteriorly, as in *Sphenodon*. This matter will be discussed later in the section devoted to muscle homologies (p. 232 ff.).

Modern urodeles possess no clavicle, since it has disappeared along with the other dermal elements as an aquatic adaptation. Its function in that group has been taken over by the greatly expanded procoracoid for the deltoid (procoracohumeralis) muscle and by the anterior edge of the scapula for the trapezius muscle. It is retained in the Anura.

Homology of the Interclavicle.—This is also lost in urodeles, but occurs in varying form as a median rhomboid, spatulate or T-shaped plate in Stegocephalia and primitive reptiles, as a variously modified or reduced T-shaped plate in most recent reptiles, and as the omosternum in all except some specialized Anura.

Homology of the Sternum.—The sternum of *Sphenodon* is a broad, shield-shaped plate, tapering anteriorly to fit the triangular notch formed by the coracoid cartilages, the posteromedial edges of which articulate with the anterior edges of the sternum by means of marginal grooves in the latter. Its rounded posterior edge articulates with three or four pairs of ventral ribs and possesses a posterior median notch. As shown by Hanson (1919a), by his own researches and by bringing together the results of many authors, the sternum of reptiles as well as of mammals, contrary to the hitherto prevalent views based on Ruge (1879), is to be regarded as an independent structure and not as a product of the fused ends of the costal cartilages. He derives it, however, from the coracoidal apparatus, but Camp (1923) regards his evidence as insufficient to support this view. Its independence of the ribs, nevertheless, seems to be clear.

The sternum of *Megalobatrachus* is a triangular cartilaginous plate with a median posterior notch and articulates in a similar way with the posteromedian edges of the overlapping cartilaginous coracoids (epicoracoids) by means of a marginal groove. It is evident that the sternum is homologous with that of *Sphenodon* and must have arisen phylogenetically in a similar way, as clearly pointed out by Ruge for Amphibia in general. Hence this structure is endoskeletal in both forms.

Eryops and other stegocephs exhibit no endoskeletal sternum in their fossil remains, for none has been preserved in any known form. As their girdle, however, indicates by its groovelike coracoidal edges the presence of a coracoidal (epicoracoidal) expansion, homologous in every way with that of later forms, it is fair to assume that the median posterior notch formed by the overlapping right and left epicoracoids was likewise filled by a triangular cartilaginous sternum (Fig. 15).

An ossified sternum and series of ossified ventral endoskeletal ribs were doubtless not needed by *Eryops* and its congeners, partly because of its semiaquatic life, and partly because it had a well-developed external support furnished by a paired, interlocking series of dermal scutes or scales, arranged in forward pointing, chevronlike rows on its ventral surface. This ventral armature, apparently common to all stegocephs, is especially well preserved in *Archegosaurus*, as shown by von Meyer's plates, one of which is reproduced in this paper (Fig. 5). It finds its homologue in the dermal abdominal ribs of *Sphenodon*, situated posteriorly to the sternum and overlapping ventrally its posterior median notched surface. These exist in certain other reptiles but less extensively,—another indication of the primitive structure of the *Sphenodon* skeleton. In *Archegosaurus*, the ventral armature continues anteriorly to a point somewhat posterior to the tapering, caudal end of the elongate rhomboid interclavicle. From here on, their chevronlike arrangement becomes reversed, so that the points of the chevrons are directed posteriorly, the rows here conforming in their arrangement about the two posterior edges of the interclavicle. An X-shaped pattern is thus formed by the scutes of this region, into the lateral spaces of which some of the forwardly directed scutes are continued, but without meeting medially. Their arrangement is such that the two latter series of scutes must have overlapped ventrally the cartilaginous coracoids, thus strengthening and supporting them, while the triangular area formed by the anterior rows of the converging series of forwardly directed scutes is in a position to have supported the inferred cartilaginous sternal plate as the epicoracoids were supported. This whole arrangement would thus account for the lack of an ossified ventral endoskeleton in the heavier-bodied semi-terrestrial stegocephs. This idea is adopted herewith in the restoration of *Eryops* (Fig. 15), the ventral scutes of which have been preserved, but not in situ.

In their reptilian descendants, because of their terrestrial habits, this contrivance developed into a complicated, well-braced girdle, while in the urodeles, on the other hand, continued aquatic adaptations involved the loss of all except the cartilaginous sternum.

Wilder has noted (1903) the tendency in *Necturus* to chondrify the medial parts of three pairs of myosepta in this region, and he regards this as the beginning of the process which in other urodeles evolved the cartilaginous sternum. He interprets it as an evidence of the primitive nature of *Necturus* (1909). It is obvious that *Necturus* is not so primitive as the branchiosaurs, and both of these are less primitive than the stego-

cephs from which they are descended. There is a progressive loss of the dermal skeleton passing from the stegocephs, to the branchiosaurs on the one hand, and to modern urodeles on the other. *Necturus* has an excessively simplified skeleton and is at the end of a line progressively more and more specialized to aquatic life, with even greater skeletal losses than *Megalobatrachus*, which still possesses a sternum. We must regard the chondrifications in the myosepta of *Necturus* as abortive attempts to produce the ventral dermal ossifications or scutes of the ancestral stegocephs, while the cartilaginous sternum has disappeared.

B. THE PECTORAL LIMB BONES OF *Eryops*, *Sphenodon* AND *Megalobatrachus*
COMPARED

Description and Homologies of the Humerus

Figures 18, 19, 20

The humerus of *Eryops* (Fig. 18, A-A'') is a short, massive bone consisting of two fan-shaped extremities set with their plane surfaces at right angles to each other on a shaft so short as to be practically negligible and forming a tetrahedral prism. Adopting Case's nomenclature (1911) for the four aspects of the bone, an outer, inner, posterior and anterior side may be designated. The proximal extremity, or head, is flattened on its outer and inner sides and is furnished with a "strap-shaped" condyle, as before mentioned. The distal extremity is flattened anteroposteriorly and spreads out to form strong, entepicondylar and ectepicondylar processes, with an articulation between for the ulna. Below the ectepicondylar process on the anterior side is the prominent, rounded, articular surface for the radius. A strong, flattened, stublike process juts out from the side of the bone, proximal and somewhat anterior to the ectepicondylar process. This may be called the "supinator process," for reasons to be discussed later. The space between the supinator process and the ectepicondylar process forms a notch, which, as may be seen from figure 20 A-F, can be homologous only with the ectepicondylar foramen of reptiles, as mentioned below. As described by Case (1911), four strong ridges bound the four sides of the short shaft, giving it a quadrangular section. In line with the ridges bounding the outer face of the humerus at their junction with the humerus head, there is a strong process above (posteriorly) and below (ventrally). These may be called, respectively, the "processus latissimi dorsi" and the "deltoid crest." Opposite the latter on the inner side of the humerus is the "pectoral crest."

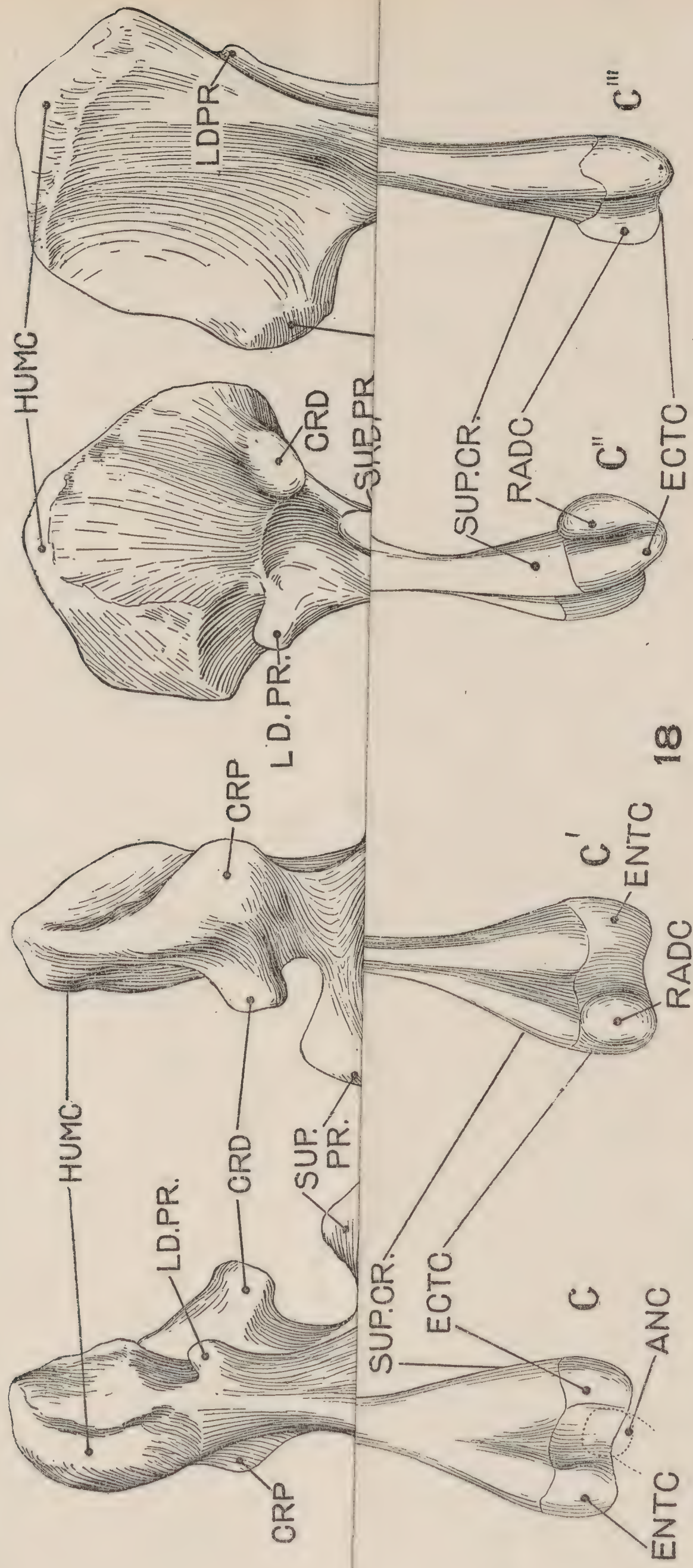


Fig. 18.—Right humerus of *Eryops* (A-A'''), *Sphenodon* (B-B'''), and *Megalobatrachus* (C-C'''), shown from posterior, anterior, outer and inner sides for comparison of homologous skeletal features.

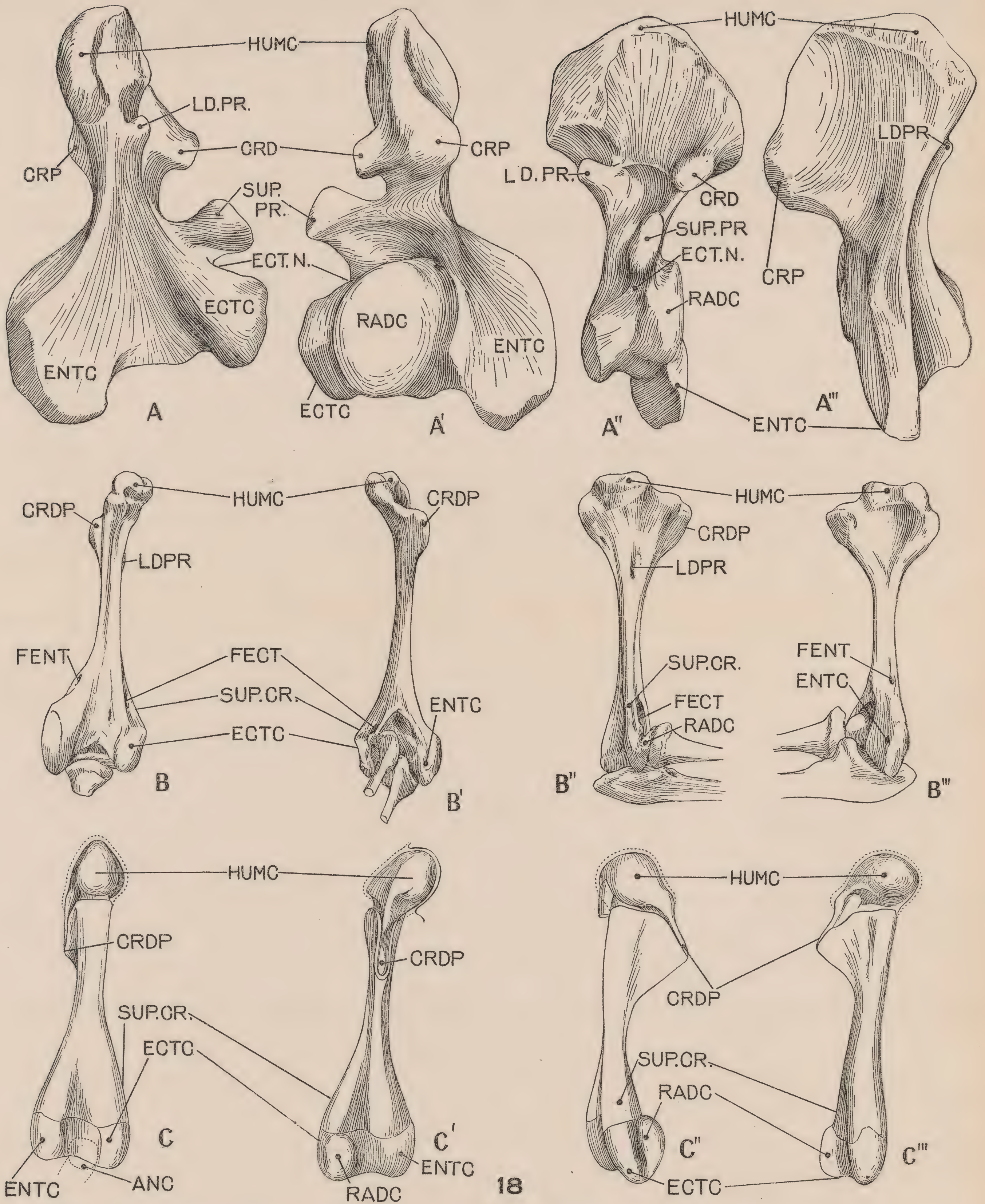


Fig. 18.—Right humerus of *Eryops* (A-A'''), *Sphenodon* (B-B'''), and *Megalobatrachus* (C-C'''), shown from posterior, anterior, outer and inner sides for comparison of homologous skeletal features.

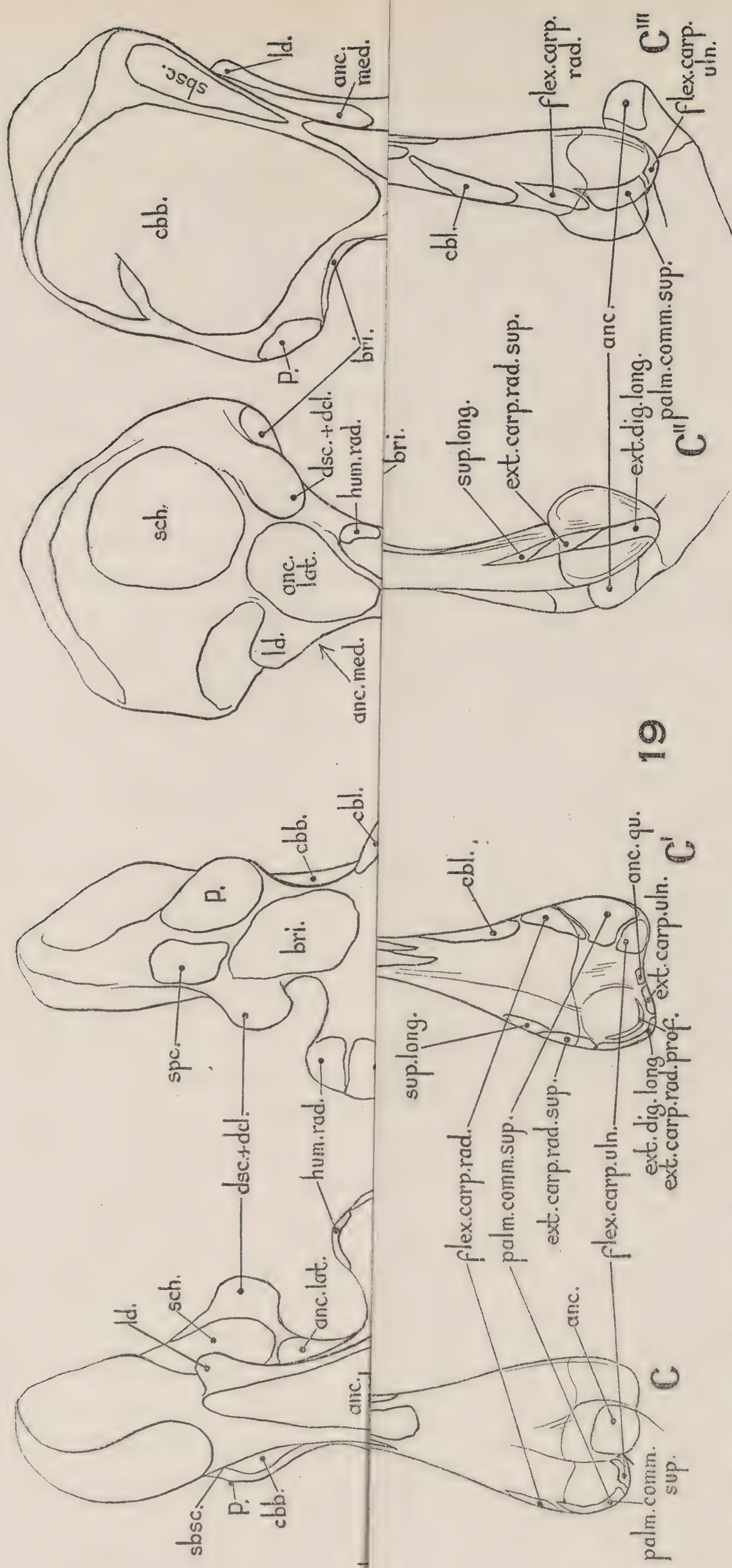


Fig. 19.—Right humerus of *Eryops* (A-A'''), *Sphenodon* (B-B'''), and *Megalobatrachus* (C-C'''), showing homologous areas of muscle attachment.

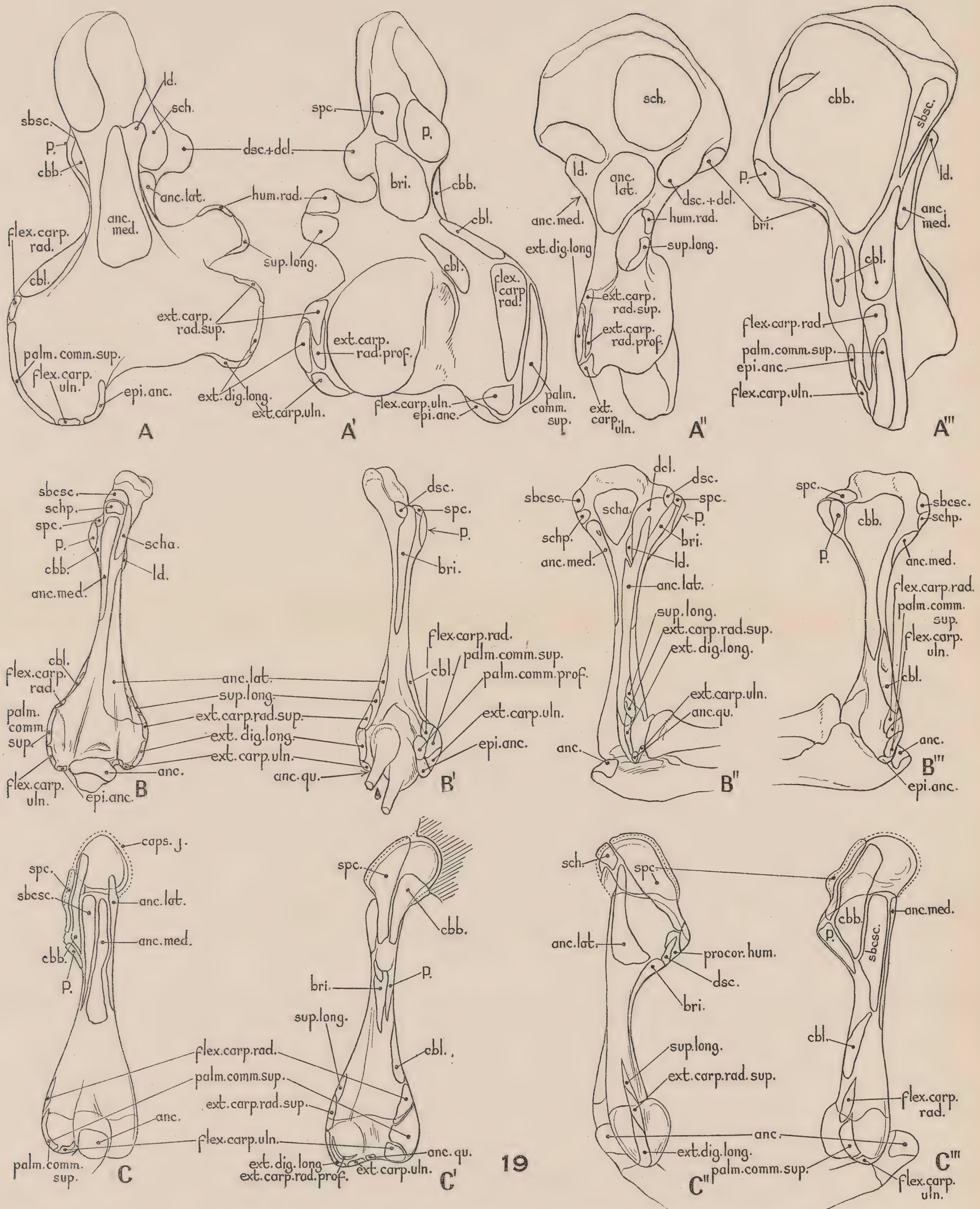


Fig. 19.—Right humerus of *Eryops* (A-A'''), *Sphenodon* (B-B'''), and *Megalobatrachus* (C-C'''), showing homologous areas of muscle attachment.

That these processes are appropriately so called is readily seen by comparing the drawings of the four sides of the *Eryops* humerus in figures 18 A to A''' with the corresponding figures of the humerus of *Sphenodon* (Figs. 18 B to B'''). If the longer shaft of the *Sphenodon* humerus be ignored, the extremities of the two bones closely correspond, the chief differences being those of proportion.

The correspondences include the caput humeri with its condyle; the processus lateralis, with its attachments for the pectoralis and deltoid muscles, ossified into the above-mentioned strong processes in *Eryops*; the eminentia m. latissimi dorsi, corresponding likewise to the processus latissimi dorsi of *Eryops*; the two epicondylar processes, and the articulatory surfaces for the radius and ulna.

The chief differences consist in the respective lengths of the shaft; the saddle-shaped condyle of *Sphenodon*, for articulating with the shoulder girdle as compared with the strap-shaped condyle of *Eryops*; the possession of an entepicondylar foramen by *Sphenodon*, entirely lacking in *Eryops*; and an ectepicondylar foramen in *Sphenodon*, as compared with the ectepicondylar notch of *Eryops* and its accompanying process.

By comparing a series of humeri like those in figure 20 A to F, the homology of this notch with the ectepicondylar foramen is clearly evident. The notch exists in practically all stegocephs, the process standing out abruptly in forms like *Eryops* (A), and *Acheloma* (B), and becoming directed distally and quite parallel with the bone in *Cricotus* (C) and *Dime-trodon* (D). In *Naosaurus claviger* (E), the outer part of the notch is bridged with bone, resulting in a foramen, which assumes its characteristic reptilian condition in such forms as *Sphenodon* (Fig. 18 B) and *Varanus* (Fig. 20 F). In the latter, it is also obvious that the proximal part of the supinator crest corresponds with the process bounding the proximal side of the notch in Permian reptiles and stegocephs, and would therefore be appropriately termed the supinator process. This is further discussed in connection with the muscles.

It is evident, then, that the various parts of the stegocephalian humerus, as exemplified by *Eryops*, are homologous with corresponding parts of the humerus of *Sphenodon*, as typical of the later reptiles. This is confirmed by comparison with many related and intergrading fossil types.

In the case of modern urodeles, adaptation to aquatic life has resulted in a lack of ossification of the condylar portions of the humerus, as shown by *Megalobatrachus* (Figs. 18 C-C'''). There is also a general

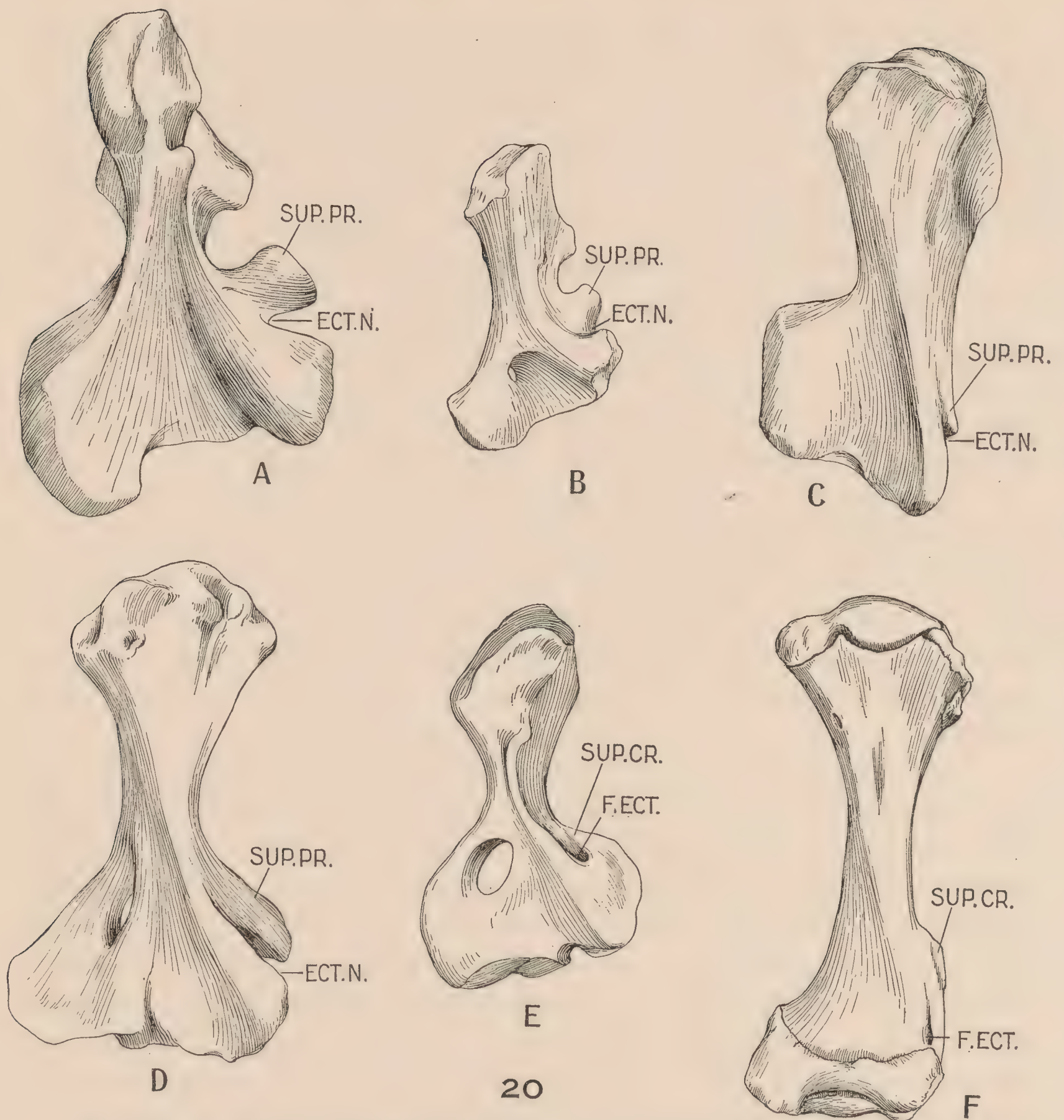


Fig. 20.—Right humeri of stegocephalian and reptilian types to illustrate evolution of ectepicondylar notch into the ectepicondylar foramen of later forms. (A) *Eryops*; (B) *Acheloma*; (C) *Cricotus*; (D) *Dimetrodon*; (E) *Naosaurus* (after Williston); (F) *Varanus*. Compare with *Sphenodon* (Fig. 18 B).

smoothness of the bone and a lack of the processes and rugosities which render homologizing easier in *Sphenodon* and *Eryops*. It is evident, however, that the bone presents the primitive “twisted humerus” type, characteristic of stegocephs, since the two extremities of the bone are at right angles. They are also of the primitive fan shape, and the ectepicondylar and entepicondylar processes are present, as well as the processus lateralis. The characteristic articular surfaces for the radius and

ulna are shown in the distal cartilage, and the shaft of the humerus is almost of stegocephalian shortness, though the proportions of the whole are more slender.

The proximal condyle, however, is unlike that of both *Eryops* and *Sphenodon* in being ball-shaped and tilted inward to articulate in a cup-shaped glenoid. As the cartilaginous extremities have not been correctly figured hitherto, so far as I can ascertain, careful drawings are shown herewith, from a large specimen preserved in alcohol. Their peculiar shape need not be described, as it is well shown in the figures (Figs. 18 A-A''').

While a number of landmarks do not appear in the *Megalobatrachus* humerus, nevertheless the different areas of the bone are readily homologized with those of *Sphenodon* and *Eryops*, and this comparison is considerably aided by a comparison of the muscles with those of *Sphenodon*, as shown later, and their areas of origin and insertion (Fig. 19). It should be mentioned here, however, that neither of the epicondylar foramina is present in *Megalobatrachus*, and there is no process or rugosity for the m. latissimus dorsi, as the latter inserts on the surface of m. anconeus scapularis in this genus.

Description and Homologies of the Radius and Ulna

The radius and ulna of *Eryops* (Figs. 7, 21) are proportionately short and stout, as compared with *Sphenodon* (Figs. 9, 17) and later reptiles on the one hand, and *Megalobatrachus* (Figs. 8, 16) and recent Amphibia, on the other. The radius is somewhat flattened and has wide extremities. The ulna articulates with radius and humerus in the usual manner. Both are well ossified, and there was probably little cartilage capping the joints, comparing well with *Sphenodon* in this respect. *Megalobatrachus*, on the other hand, has an entirely cartilaginous olecranon projecting well above the distal end of the humerus. The cartilage capping the radius, however, is comparatively thin. The homologies of these bones in all three forms are self-evident.

Description and Homologies of the Carpus

The carpus of *Eryops* (Figs. 7, 21) contains eleven bones, that of *Sphenodon*, ten (Figs. 9, 17); while there are but seven unossified elements composing the wrist of *Megalobatrachus* (Fig. 8). Radiale, ulnare and intermedium are obviously homologous in the three animals. There are five distal carpalia in *Sphenodon*, one for each of the five digits. These have been reduced to three in *Megalobatrachus*, one having been lost with

the fifth digit, and that for the first having probably fused with the second carpal, as both share in its articulation. As shown by Gregory, Miner and Noble (1923), *Eryops* also possessed but four true distal carpals, the fifth having been lost with the fifth digit, or reduced to a sesamoid cartilage, for which a facet shows on the ulnar-distal corner of the ulnare, though the cartilage has not been preserved.

The *Eryops* carpus has a large centrale articulating with the radius between the radiale and the intermedium, thus leaving three medial carpals, forming a row from the radial side of the carpus, between the distal carpalia distally and the radiale and centrale proximally. These are termed medialia 1, 2, and 3, by Gregory, Miner and Noble, following Schmalhausen (1917) for the tarsus of *Ranodon sibericus*.

The *Sphenodon* carpus (Figs. 9, 17) has two centralia, which may either be homologous with the three medialia of *Eryops*, through the fusion of two, while the true centrale fused with the intermedium; or the more ulnar of these may be the true centrale, crowded out of place by the ulnare and intermedium, while the more proximal represents the three medialia fused; or the other two may have been lost.

Megalobatrachus (Fig. 8) has a single centrale, all the medialia having been fused with other elements, or lost, the latter being more likely because of the general reduction of the skeleton.

Description and Homologies of the Manus

Sphenodon (Figs. 9, 17) has five digits, the typical number for the tetrapod limb. All the known Amphibia (Fig. 8) have but four, but embryological investigations show (see Steiner, 1921, 1922) that in this group the embryonic blastoderm starts the development of a fifth finger which soon disappears. Since this occurs in both Anura and Urodela, the pentadactyl hand like the pentadactyl foot is a fundamental feature of the entire group and was inherited from the common ancestor of the amphibians and reptiles, somewhere among the embolomorous Stegocephalia. Until recently, it was supposed that *Eryops* represented this pentadactyl ancestor. This idea was based on a specimen of the carpus in the American Museum of Natural History (A. M. N. H. No. 4186), which is the best preserved known, in which a digit is shown associated with distal carpalia 1, 3, 4 and 5, as they have been considered until recently, when von Huene (1922) suggested that the first digit had been displaced in fossilization. Examination of the specimen showed that this was correct, and Gregory, Miner and Noble have collaborated in a paper (1923), in which the matter is discussed in detail, a new reconstruc-

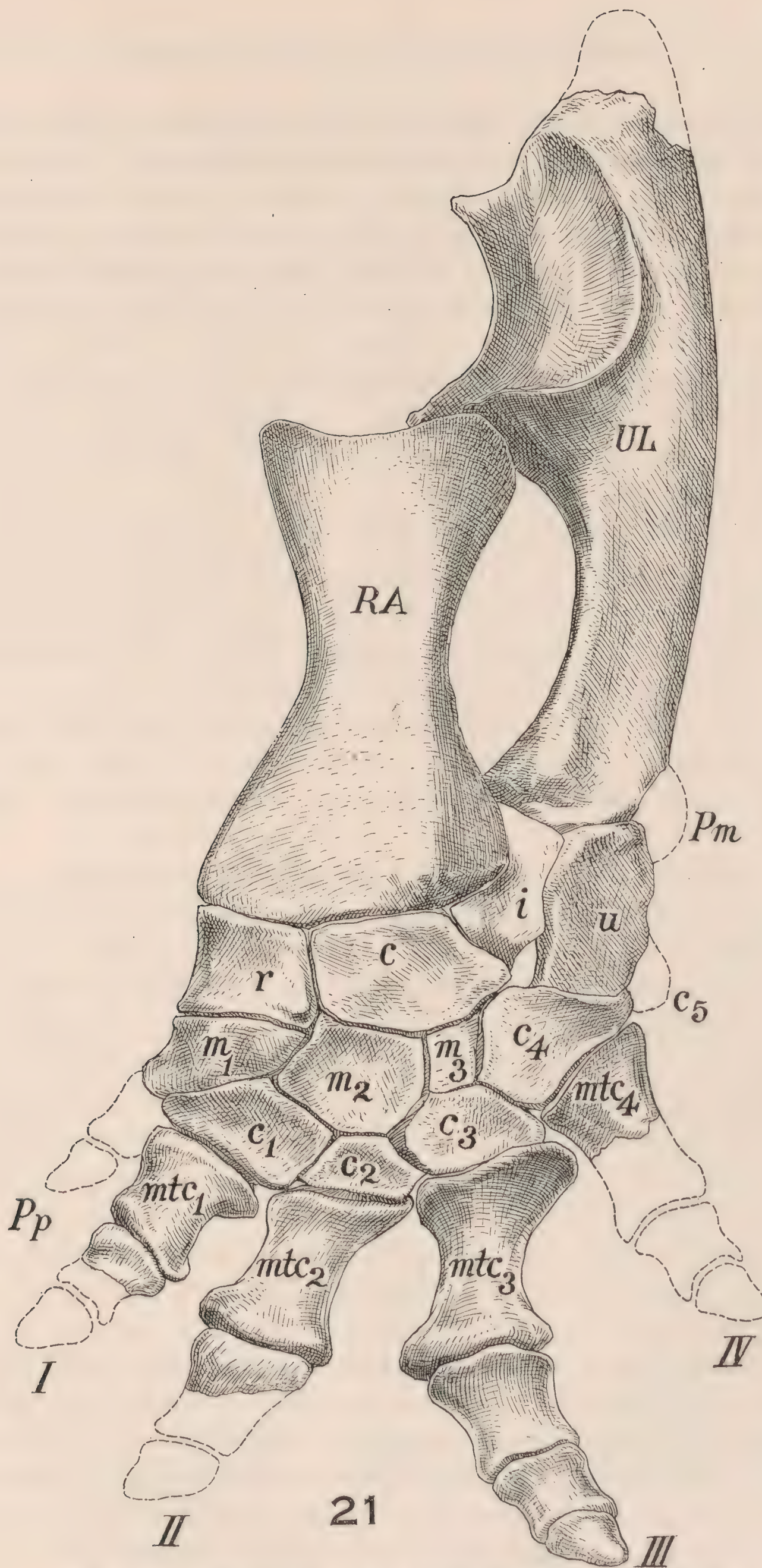


Fig. 21.—Restoration of left antibrachium and manus of *Eryops*, drawn in perspective from a study of the original specimen, A. M. N. H. No. 4186. See text for description.

tion made of the skeleton (Fig. 21), and its significance correlated with the recent embryological work of various investigators. I was able to test this further in connection with the restoration of the muscles of the carpus of *Eryops*, with confirmatory results, as will be shown later in this paper (pp. 258, 266, 273, 274, 278, 290, 291). A summary of the conclusions reached by the collaborators is all that need be given here. They are as follows.

(1) The first digit was found to fit on the second distal carpal, while the first was too small for articulating a functional digit. Hence the number of digits in *Eryops* was demonstrated to be four instead of five, as in all known Amphibia.

(2) There is, nevertheless, a distinct but small articulation on the first distal carpal, which can have been associated only with a prepollex, thus confirming the view of Gregory (1915) that all true digits are associated with the ulnar pyramid of carpals. This is further confirmed by the investigation of the musculature in this paper.

(3) Embryological and paleontological evidence favor the view that the most primitive stegocephalian Amphibia had five digits and a post-minimus in the hand, which points to a six-rayed primitive pectoral tetrapod limb.

(4) There is no reason in the fossil material to assign a greater phalangeal formula to the *Eryops* manus than 2-2-3-2, the typical urodele arrangement.

The accompanying figure (Fig. 21) shows the reconstruction of the *Eryops* antebrachium, as thus worked out. It will be noted that for the first time, through a proper arching of the carpus, the carpal bones have been made to fit; that the notch of the intermedium articulates with the ulnar-distal angle of the radius on its ventral side; and that there is a foramen surrounded by the intermedium, ulnare, carpal 5 and the centrale. The articulation on the mediale is the evidence for a prepollex, which may have had but one joint, but which is here tentatively assigned two on the ground that the articulation indicates that it was partly functional and may have even reached the ground.

A terminal phalanx must be assigned to digit I, since the fragment preserved is clearly not a terminal one. It is too small to make more than that likely. The same argument applies to digit II.

Digit III is preserved complete with three phalanges. Metacarpal IV is represented only by the stump of a metacarpal, which is sufficiently large to assign it two phalanges by comparison with digit II.

Articulatory surfaces make it necessary to postulate a vestige of digit V, and a pisiform, which is assignable to an original digit VI or postminimus.

The only possible method of articulating the phalanges indicates that I and II were directed radially, while III and IV were directed ulnarward, diverging strongly from I and II. The carpus was doubtless partly supported by a pad ventrally.

The arch of the carpus is indicated by the articulatory surfaces of the carpal bones, which converge ventrally, so that the flexor surface of each is smaller than the dorsal surface, with the exception of the radiale and mediale. In fossilization, the carpus was flattened so that the articular surfaces were mostly separated ventrally, though the bones remained in contact dorsally.

The metacarpals are much shorter in *Eryops* than in either *Sphenodon* or *Megalobatrachus*. This is true of the phalangeal elements as a whole and is a primitive feature.

The phalangeal formulæ are as follows.

<i>Eryops</i>	2-2-3-2
<i>Megalobatrachus</i>	2-2-3-2
<i>Sphenodon</i>	2-3-4-5-3

By a comparison of these, it is evident that in both urodeles and reptiles the outer side of the hand is more important functionally. Apparently, the greatest muscular energy is directed to the outer side of the foot in both lines of descent. This is correlated with the arrangement of the carpal elements, of which the greater number form a pyramid of support for the base of the ulna as indicated above. It is also evident, from a comparison of the number of phalanges, that terrestrial reptiles have practically preserved the primitive phalangeal formula. In the earliest reptiles, such as *Eosaurus* and *Limnoscelis*, the formula is 2-3-4-5-4. In modern terrestrial reptiles all are retained, except for the dropping of a single phalanx in digit V. In the most primitive amphibian, on the other hand, as well as in those of recent times, we have the formula 2-2-3-2 in the manus. This may be due to the beginning of aquatic specialization shown in skeletal reduction of the foot, and is a part of the same process which caused the total loss of digit V throughout the group.

SECTION II. MUSCULATURE

A. MUSCLES FROM BODY TO SHOULDER GIRDLE

Trapezius and Sternocleidomastoideus

Figures 22 to 27

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> a. As single muscle b. Posterior part of skull (medial part of squamosal bone) c. Dorsal fascia	<i>Origin</i> a. As more or less double muscle b. Posterior part of skull (squamosal, parietal and supraoccipital bones). —[The smaller, anterior portion (sternocleidomastoideus)] c. Mostly from neck fascia from skull to 8th or 9th vertebral segment.—[The larger posterior portion (trapezius proper)]
<i>Insertion</i> Narrow, but including whole anterior border of bony scapula as far as junction with cartilaginous procoracoid	<i>Insertion</i> a. Sternocleidomastoideus. Lateral two-thirds of clavicle b. Trapezius—Narrow insertion on acromion
<i>Innervation</i> Branch from ramus intestinalis of vagus	<i>Innervation</i> a. N. Vagoaccessorius b. 4th, 5th and 6th spinal nerves

From the above comparison it is clear

(1) That in both *Megalobatrachus* and *Sphenodon* a muscle suspends the anterior border of the pectoral girdle from the posterior region of the skull and the anterodorsal fascia of the back.

(2) That in both these cases there is an innervation from the vagoaccessorius nerve belonging to the visceral system.

(3) That, while in *Megalobatrachus* (Fig. 25) this muscle is single, and is innervated solely by the vagoaccessorius nerve, in *Sphenodon* (Figs. 24, 26) it is more or less split into two muscles, and, in addition to an anterior visceral innervation, receives a considerable posterior innervation from spinal nerves of the somatic series, i.e., the ventral rami of the 4th, 5th and 6th spinal nerves.

Fürbringer has shown (1900, p. 400) that, in recent Lacertilia, the trapezius and cleidomastoideus, in the simplest condition, form a single

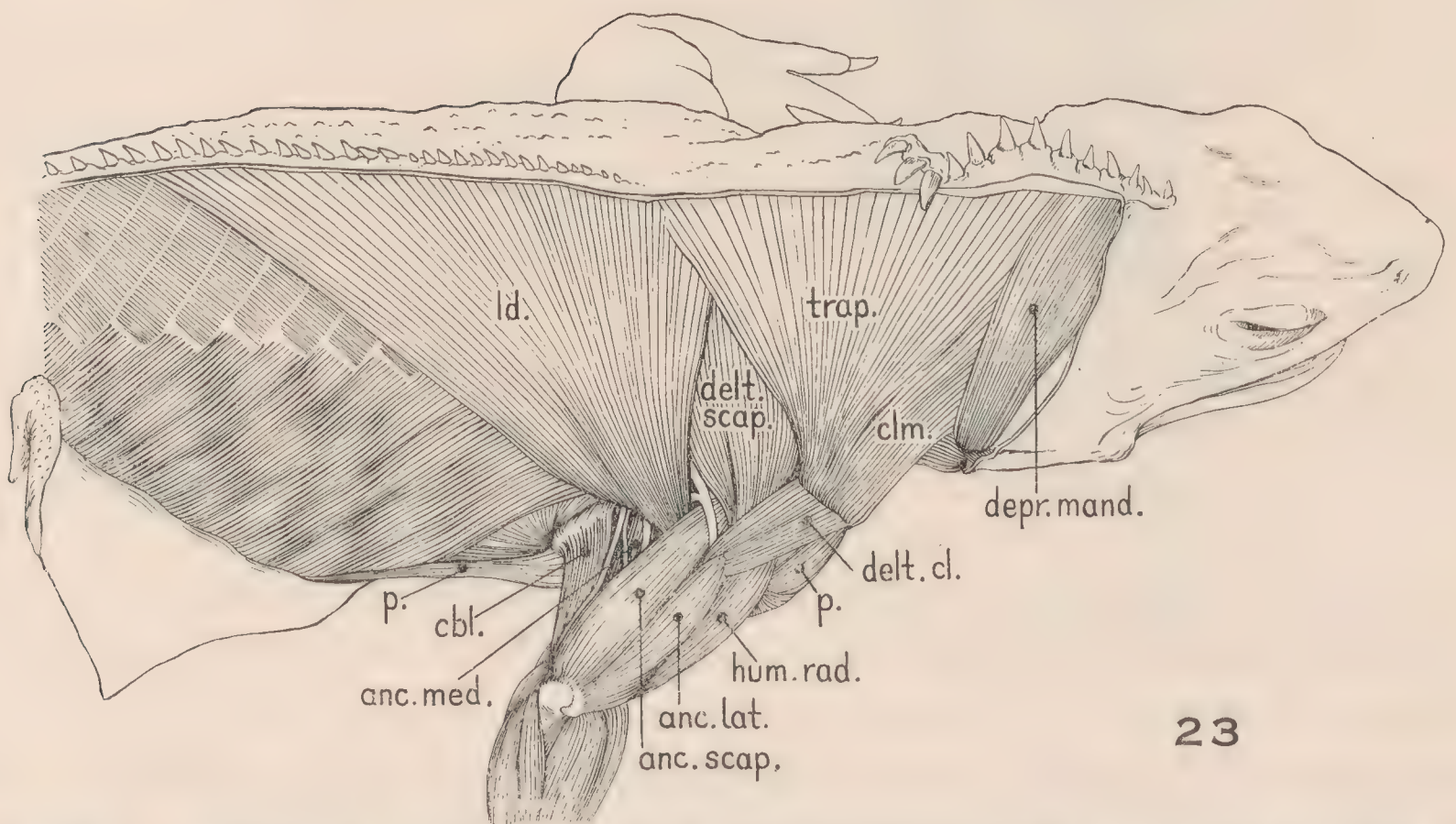
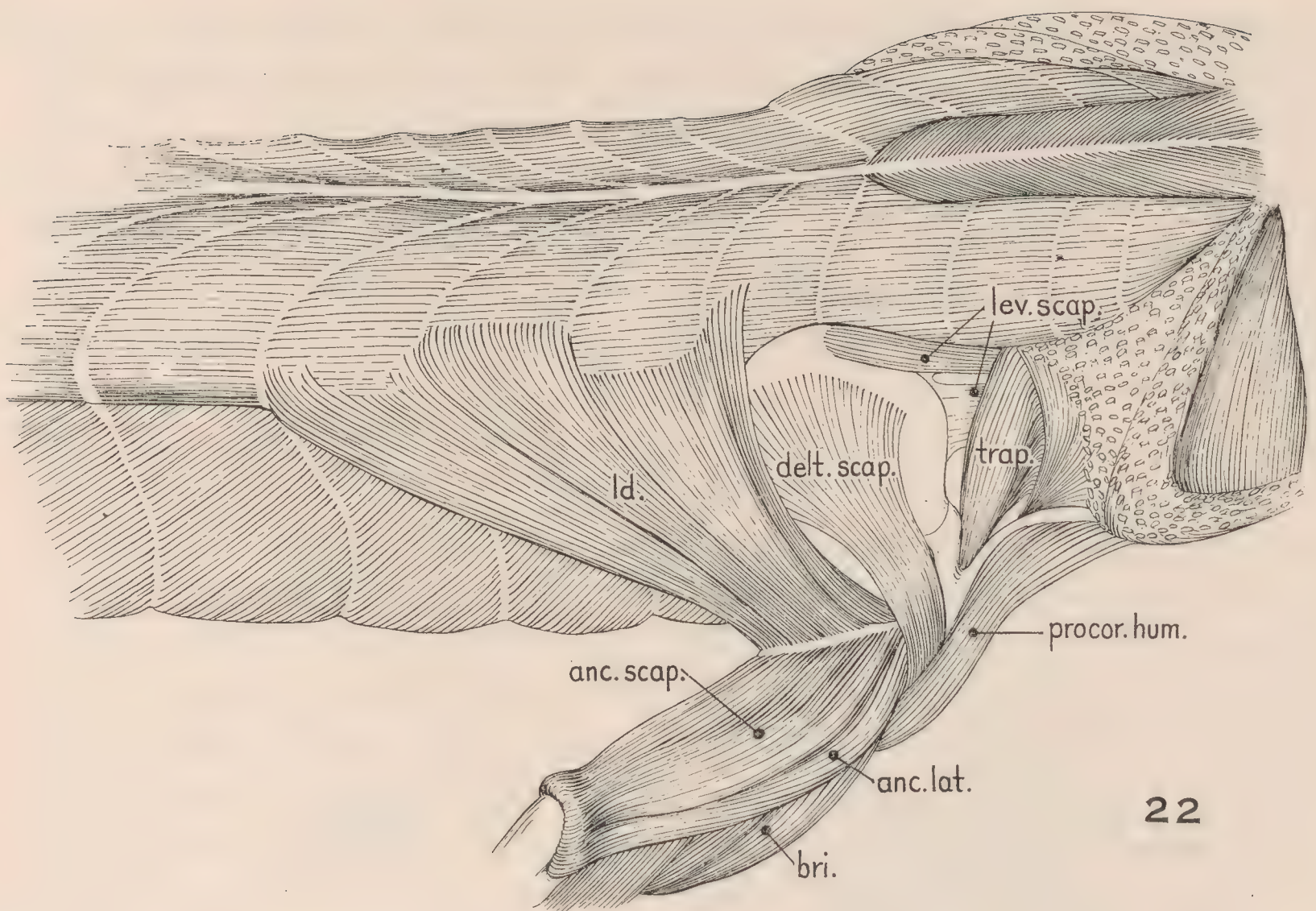


Fig. 22.—Dissection of the superficial dorsal musculature of shoulder girdle and upper arm of *Megalobatrachus maximus*.

Fig. 23.—Dissection of the superficial dorsal musculature of shoulder girdle and upper arm of *Sphenodon punctatus*.

muscle mass. From this state of affairs, there is a continuous series of examples in the various genera of the group showing a gradual separation into two distinct muscles culminating in *Phrynosoma* as the most extreme type. In all cases, the anterior slip (cleidomastoideus) originates as in *Sphenodon* from the rear of the skull, while the insertion tends to include not only the clavicle but the transverse projections of the episternum as well. In every case also, the innervation of this muscle is

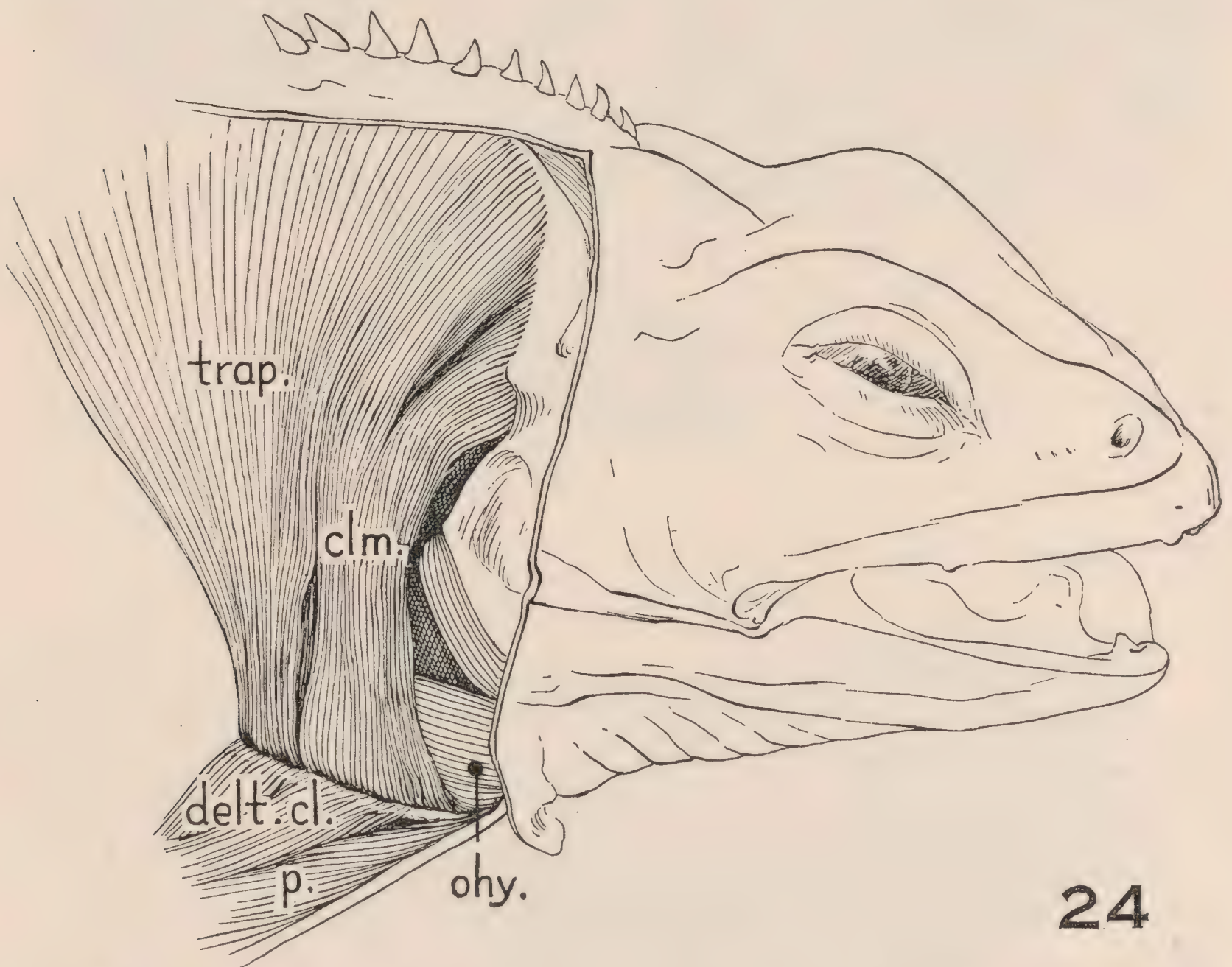


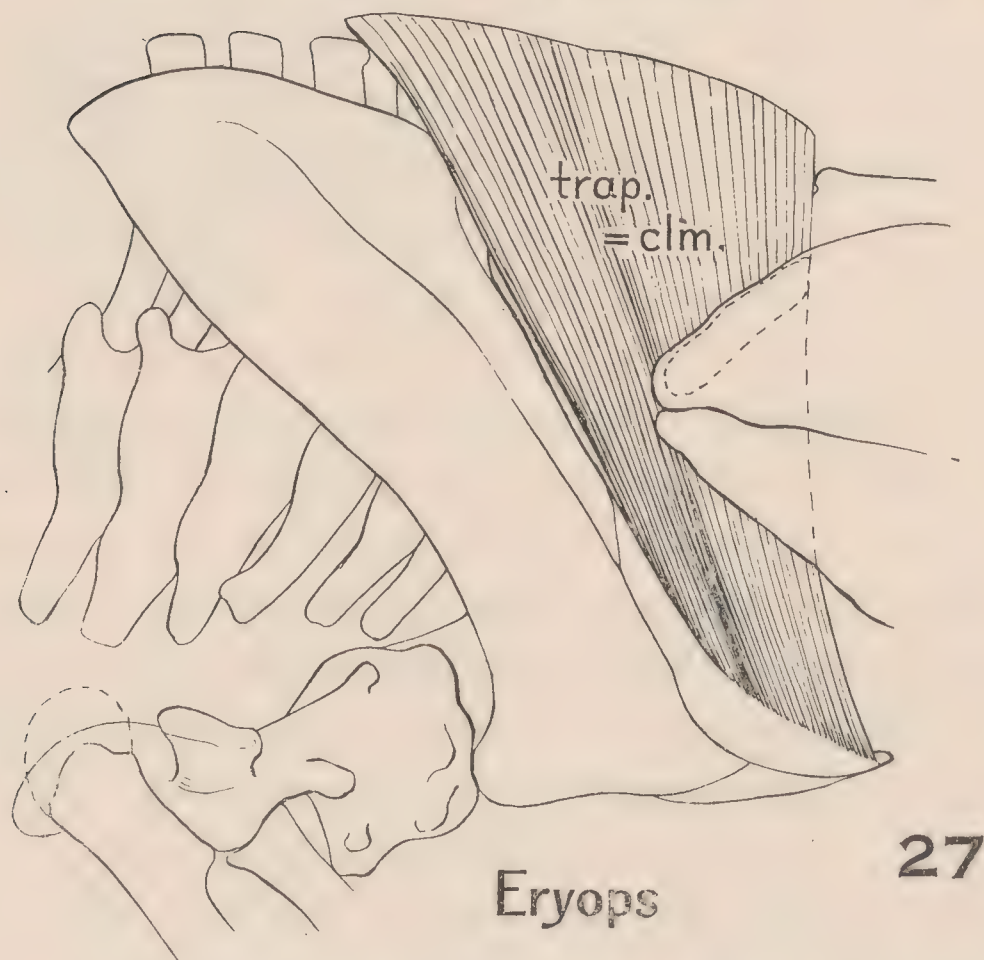
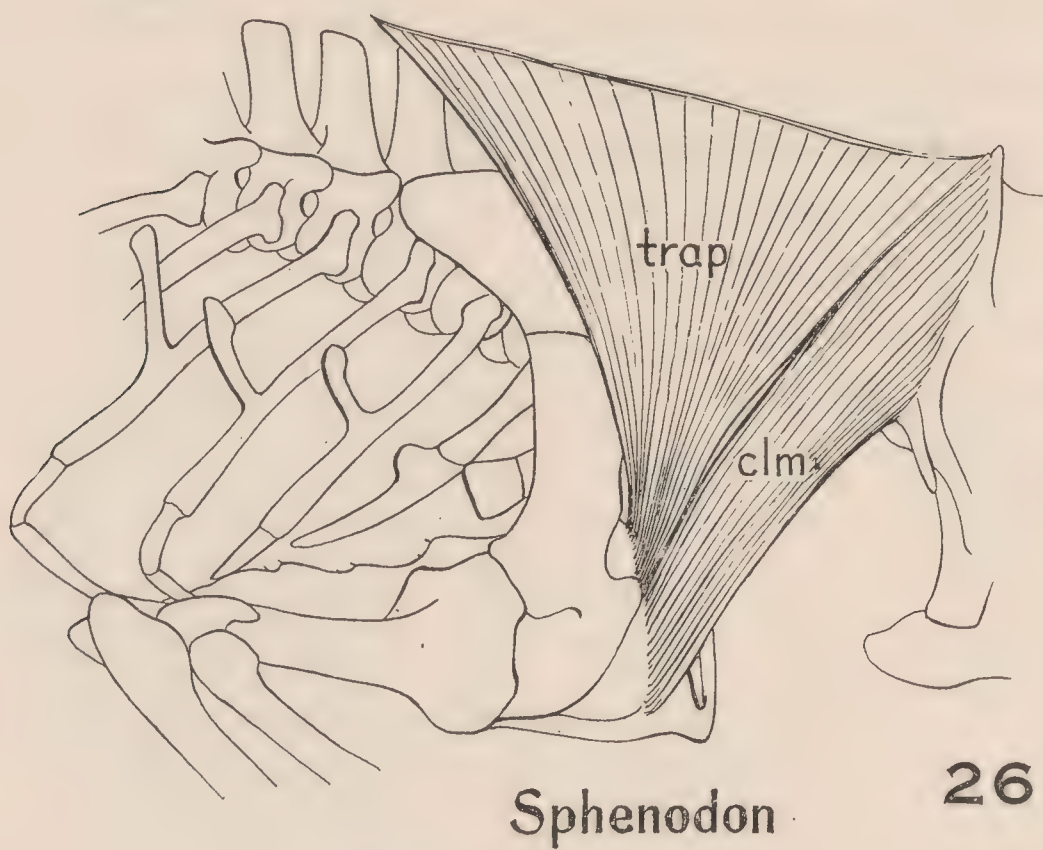
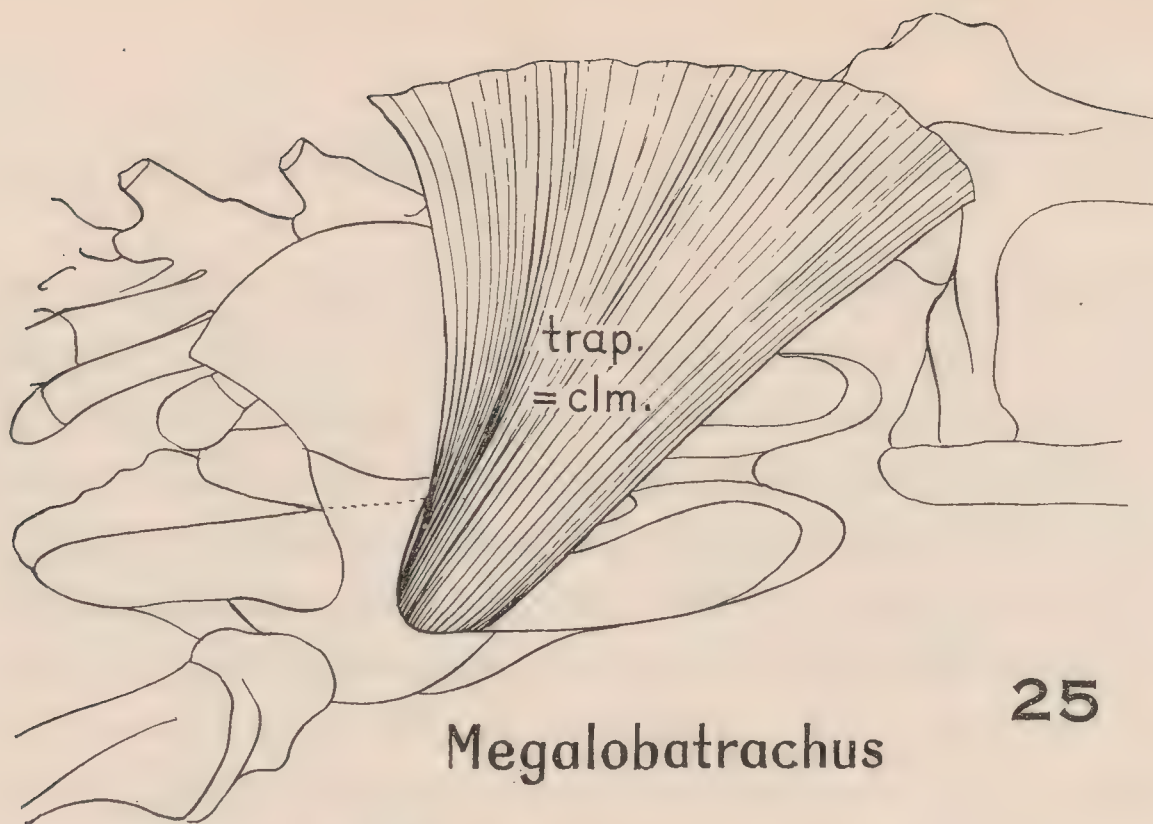
Fig. 24.—Dissection showing incomplete separation of trapezoid and cleidomastoideus muscles in *Sphenodon*.

largely visceral, but with some spinal somatic fibres included. The trapezius proper throughout is innervated by spinal somatic nerves from a varying number of segments, corresponding to the number of muscle somites included in its backward extent. It is evident, therefore, first, that the incompletely separated condition of the muscle mass in *Sphenodon* is a primitive character as compared with the other modern reptilian groups, and, secondly, that its complex innervation is typical of the modern reptiles as a whole.

In the urodele Amphibia, on the other hand, the muscle is single, comparatively narrow, and is innervated entirely by the vagoaccessorius nerve and hence belongs to the visceral series. In *Megalobatrachus* and the most typical modern urodeles, the most important and most fleshy part of the origin is from the skull, though in branchiate forms more specialized for aquatic life, like *Necturus* (Wilder, 1912, p. 389), the attachment to the skull has been secondarily lost, while the visceral innervation remains. The condition in *Megalobatrachus* is doubtless primitive, since it is correlated with the anterior position of the girdle and short neck, as in the Stegocephalia. Among the reptiles, with the advent of terrestrial life, the disappearance of the gills, the consolidation of the former gill arches into the hyoid apparatus and the lengthening of the limbs, the neck became more important functionally. This resulted in a retreat of the anlagen of the pectoral limbs and, hence, the inclusion of a greater number of vertebræ in the neck, while the greater demands made upon the limb muscles by the progressively more active terrestrial life caused in the case of trapezius a posterior expansion of the muscle mass, by the inclusion of contributions from the myotomes of the neck, together with their somatic innervation. Hence the only part of this muscle complex that can be considered homologous to the trapezius of *Megalobatrachus* is that portion of the cleidomastoideus innervated by the vagoaccessorius nerve (Fürbringer, 1900).

The simple trapezius of *Megalobatrachus*, with its visceral innervation, is directly comparable to a similar muscle in *Acipenser* (except *Acipenser sturio*, where it is secondarily absent—Meissner, 1908), *Polypterus*, the Elasmobranchii, Holocephali and Teleostii generally (Shann, 1921), where it arises from the rear of the skull and inserts into the anterior border of the scapula and, in bony fishes, on the cleithrum as well. It is innervated by the intestinal branch of the vagoaccessorius.

The trapezius in *Megalobatrachus* shows an intermediate condition between the fishes and the reptiles and, hence, may be held to more nearly represent the status of this muscle in *Eryops* and the stegocephs generally (Fig. 27). Here it must have been a narrow muscle because of the anterior position of the girdle, and the weight of the body must have necessitated a posterior expansion of the muscle so far as the girdle allowed, as well as a strong suspension from the squamosal and the posterior part of the skull generally. Its insertion seems to have been on the ventral part of the cleithrum, the clavicle and lower anterior border of the scapula. The innervation was doubtless through the vagoaccessorius nerve, as in fishes and amphibians generally.



Figs. 25, 26, 27.—Comparison of the trapeziuscleido-
mastoideus musculature in *Megalobatrachus* and *Sphenodon*,
and the homologous musculature as inferred for *Eryops*.

The exceptional character of the trapezius muscle in being the only visceral muscle attached to the shoulder girdle, throughout the vertebrate groups, has always been perplexing. Johnston (1906, p. 203) adduces it as ground for supporting Gegenbaur's theory of the origin of the girdle from a branchial arch, though he apparently applies this only to the girdle itself and not to the limb, and of course makes no attempt to extend the application to include the pelvic arch, which has no such innervation. The evidence adduced by the majority of modern writers in supporting the fin-fold theory has effectually disposed of the possibility of the gill-arch theory but has not, so far as the writer is aware, explained the innervation of the trapezius. The following considerations are therefore offered as throwing some light on this difficult subject.

(1) In *Megalobatrachus* the trapezius is located posteriorly and medially to the series of branchial muscles comprising in order the levatores arcuum II, III, IV, hyotrachealis, dorsotrachealis and dorsolaryngeus, and is so placed as to form the last and innermost of the series.

(2) All these muscles are innervated from the intestinal branch of the vagus.

(3) Hence all, including the trapezius, should be included in the same group.

(4) The origin of the scapulocoracoid from the outer mesenchyme of the body (Osburn, 1907, p. 431) precludes its being grouped with the visceral arches which arise from the splanchnic mesenchyme.

(5) Hence we are led to the inference that the trapezius is derived from the musculature of a vanished gill arch, formerly existing posterior to the fifth gill arch of most modern elasmobranchs and fishes in general.

(6) The possibility of additional gill arches in primitive elasmobranch types is evidenced by the survival of such forms as *Hexanchus* and *Heptanchus*, and, if it be objected that their supernumerary arches are secondarily acquired and that one of the most ancient fossil sharks known, *Acanthodes*, from the Coal Measures, had but five gill slits, it may be noted that this shark was regarded by Smith Woodward as a member of a highly specialized Paleozoic group, while *Cladoseleache*, from the Lower Carboniferous, had at least seven, and probably nine gill slits, according to Dean (1895), and is regarded by him as probably ancestral to such forms as *Acanthodes* (Dean, 1895, pp. 78 to 81).

(7) This view is also borne out by embryological evidence. Miss Hawkes (1905) found vestiges of a sixth branchial arch in two recent species (*Gyropleurodus francesci* Girard and *Heterodontus phillipi* Blainville) of the family Heterodontidæ, which was abundant in Paleo-

zoic seas. Thus there is clear evidence for previously existing visceral arches to which the trapezius muscle could have been attached.

(8) Osburn has observed (1907, p. 429) that "the pectoral girdle of *Cestracion* [one of the genera investigated by Miss Hawkes] as it develops moves toward the gill-region. When it first appears, the scapular portion of the girdle is separated from the last gill arch by a considerable space, but as development proceeds the girdle and the arch approach each other until the intervening space is eliminated. At first this space is fully twice as great as that between the gill arches; at 60 mm. the arch and girdle are practically in contact. In the adult they overlap slightly."

This observation is highly significant, though used by Osburn in a different connection. It is what one would expect as an ontogenetic record of the migration forward of the pectoral arch to occupy the place of a disappearing gill arch.

(9) On these grounds it is possible to suggest that the ancestral elasmobranchs possessed more than five gill arches; that, through the well-known tendency toward consolidation in the direction of the head-region (evidenced among other phenomena by the gathering together of posterior nerve roots to form the vagoaccessorius nerve trunk), the pectoral girdle migrated forward, interfered with the sixth gill opening, and crowded it and its arch until they degenerated and disappeared in situ. In this process the insertion of the levator arcus VI musculature and perhaps other slips were taken over by the anterior border of the girdle, together with its post-trematic visceral nerve supply, to form the trapezius branch of the intestinal ramus of the vagoaccessorius nerve.

Levator Scapulæ

Figures 28 to 30

The similar origin, insertion and innervation by the spinal nerves show that these muscles in Amphibia and Reptilia are generally homologous. The similar location with reference to other muscles is an argument in the same direction.

The principal differences are as follows.

(1) The origin in *Megalobatrachus* (Fig. 28) is from the pharynx wall, while in *Sphenodon* (Fig. 29) it is from transverse vertebral processes.

(2) In *Megalobatrachus* the muscle is single; in *Sphenodon* it is double.

(3) In *Megalobatrachus* the ventral three-fourths becomes aponeurotic before insertion, only the dorsal fibres continuing to their attachment on the suprascapula (Figs. 28, 53).

(4) The innervation in *Megalobatrachus* includes visceral nerves from the vagus nerve trunk, while that in *Sphenodon* is wholly somatic.

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> From connective tissue of pharynx wall near the base of the skull as a ribbonlike band. A single muscle	<i>Origin</i> Transverse processes of 1st and 2d vertebræ. A single origin immediately dividing into two slips
<i>Insertion</i> Dorsal portion as a narrow strand on the outer surface of the vertebral border of the suprascapula; the ventral three-fourths becomes aponeurotic and inserts on the anterior border of the suprascapula as a membranous continuation of the dorsal portion	<i>Insertion</i> a. Superior. Anterodorsal part of outer surface of suprascapula b. Inferior. Anterior edge of bony scapula near the acromion and the most dorsal part of the clavicle
<i>Innervation</i> Small nerves from Ramus intestinalis vagi, hypoglossus (N. spinalis I), and N. spinalis II.	<i>Innervation</i> Nn. spinales IV, V (VI)

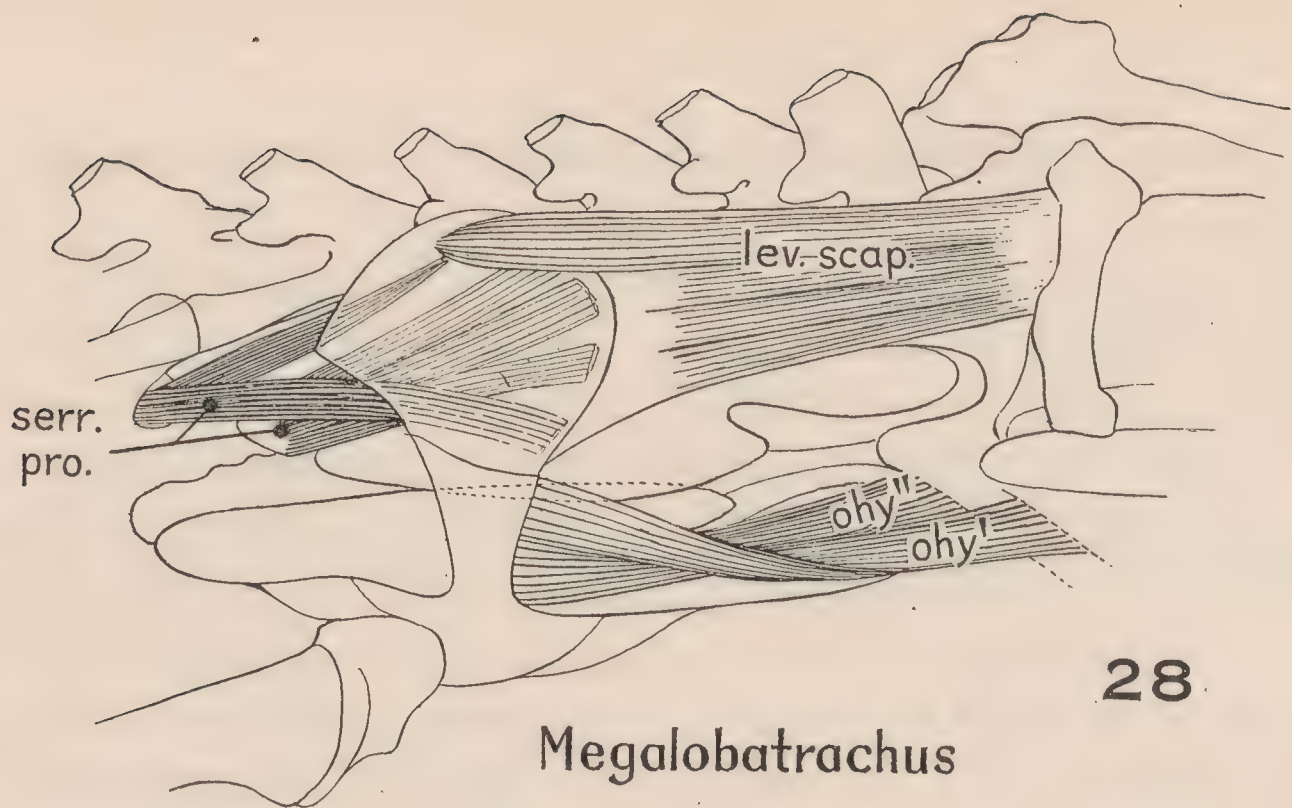
Each of these points, when examined, is significant. They will therefore be taken up in order.

(1) The origin of the muscle in the neighborhood of the fascia of the pharynx brings this part of the muscle into intimate relation with the muscles of the pharyngeal system. This suggests a comparison with the visceral muscle system.

(2) The single condition of the muscle in *Megalobatrachus* is primitive as compared with the differentiation into two slips in *Sphenodon* (Fig. 29).

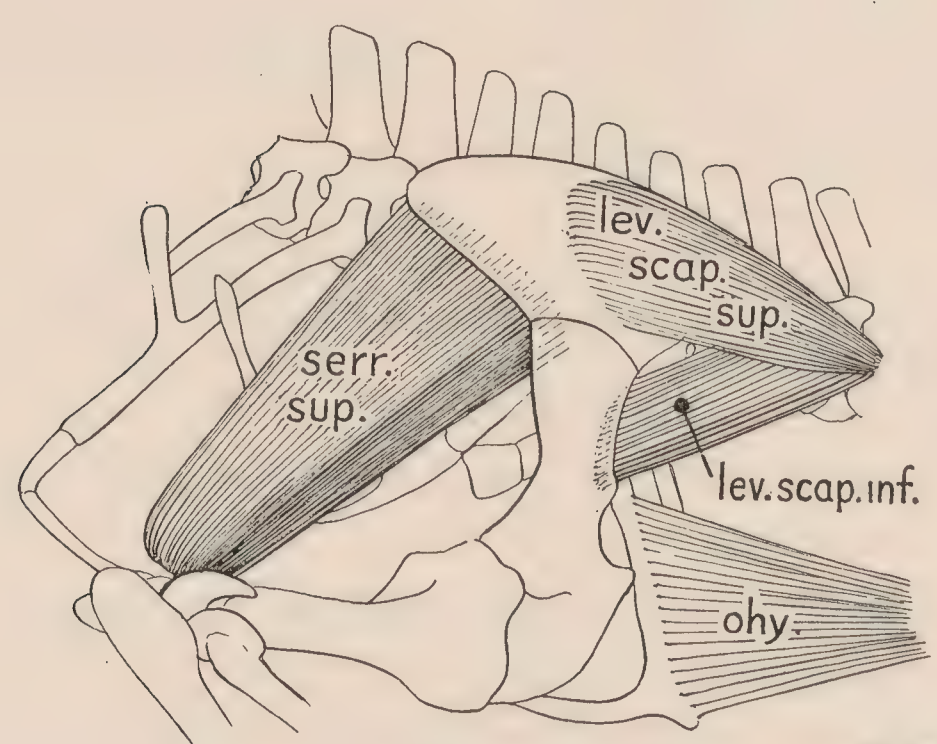
(3) The tendency to become aponeurotic toward the insertion seems to be correlated with the lessened stress on the girdle in an aquatic animal and may be looked upon as an aquatic adaptation.

(4) A comparison of the innervations indicates that the history of the levator scapulæ is similar to that of the trapezius. The suggestion is offered that it represents the deeper portion of the "trapezius" muscle, described by Shann and Vetter (Shann, 1919, p. 550) for Holocephali, and by Shann and earlier writers as one of the deeper portions of the trapezius of selachians. It is described as innervated by the vagus nerve. In fishes generally there is a great development of the anterior protractor and levator pectoralis systems, extending from the cleithrum and scapula to the base of the skull, and more deeply from the posterior



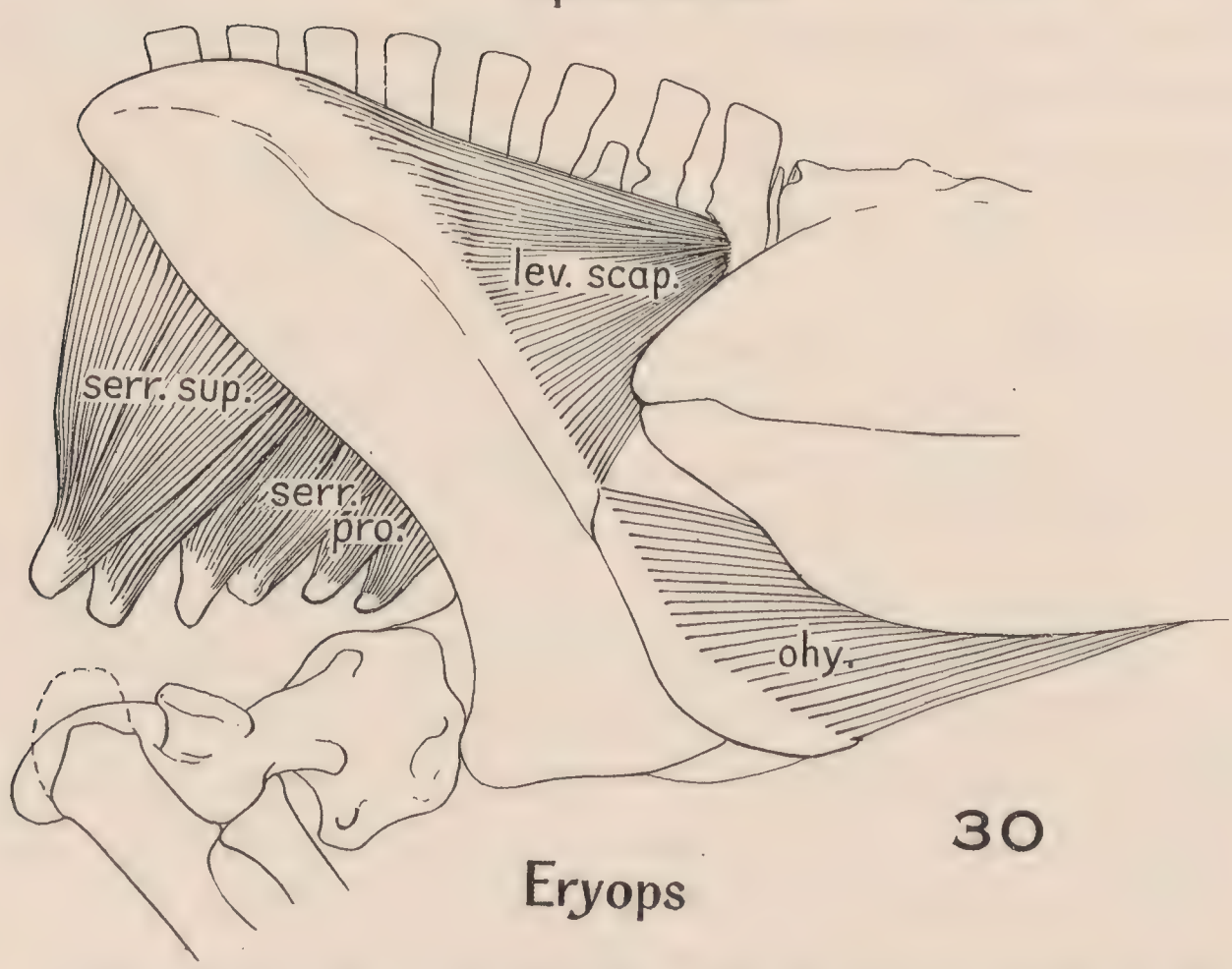
28

Megalobatrachus



29

Sphenodon



30

Eryops

Figs. 28, 29, 30.—Comparison of the levator scapulæ, omohyoideus, and serratus systems in *Megalobatrachus* and *Sphenodon*, and their restoration as inferred for *Eryops*. The serratus profundus system of *Sphenodon* is shown in figure 32.

branchial arches. The trapezius and levator scapulæ are interpreted by me as representing the remainder of this system in urodeles as exemplified by *Megalobatrachus*, and that, as in the case of trapezius among reptiles, there has begun a taking over of this muscle by the somatic system, through a posterior addition of spinally innervated muscle elements from the anterior trunk myotomes. This is carried further in reptiles as represented by *Sphenodon*, where the visceral portion of the muscle has been entirely lost in correlation with the posterior "migration" of the pectoral girdle, and the muscle is innervated solely by the 4th, 5th and 6th spinal nerves.

As shown in the discussion of the trapezius muscle, the latter, in *Sphenodon*, is in the stage of evolution of the levator scapulæ in *Megalobatrachus*, so far as innervation and composition of the muscle are concerned.

Earlier writers, for example, Osawa (1902, p. 270) and Humphry (1872, p. 31), mention the levator scapulæ of *Megalobatrachus* as a narrow strandlike muscle inserting on the vertebral border of the suprascapula. My dissections show, however, that the muscle is quite fleshy and broad (8 mm. in the specimen examined) during the greater part of its course, but the change to an aponeurotic condition of the ventral portion as it nears its insertion causes it to appear quite narrow upon superficial examination.

As the stegocephalian group is ancestral to both Amphibia and Reptilia and is intermediate between the fishes and the higher vertebrates, the condition of this muscle in *Eryops* (Fig. 30) should involve the features common to *Megalobatrachus* and *Sphenodon*, and where they differ should incline toward the more primitive side, to which it should be more directly prophetic. Due allowance should be made for the secondarily aquatic features and for the retention of the dermal girdle in *Eryops*, including the piscine cleithrum.

The inferences are as follows.

(1) The muscle was single in *Eryops*, as representing the deeper trapezius layer of fishes, on the one hand, and the single condition of the muscle in urodeles, on the other.

(2) It was inserted in the cleithrum as in fishes.

(3) It is represented as originating from the transverse process of the anterior vertebræ, as well as from the pharynx wall, because it would seem that greater ossification of the heavy skeleton of *Eryops* and the weight of its body would require a firm attachment like that found in *Sphenodon*, while partially retaining the close association with the visceral musculature inherited from the fishes and perpetuated in the urodeles.

(4) It did not extend far down on to the clavicle, thus agreeing with *Sphenodon*, in which the attachments of both slips are practically dorsal to that feature and occupy the position of a cleithrum, which has disappeared. In this connection, it may be remarked that the specialization of the levator scapulæ into two slips in *Sphenodon* may be correlated with both the differentiation of the scapular blade into the bony scapula proper and the cartilaginous suprascapula, as well as the tendency of the dorsal portion (pars superior) to insert on the lateral face of the girdle, and of the ventral portion (pars inferior) to insert on the medial face.

(5) There was no tendency to become aponeurotic as in *Megalobatrachus*, since this is a secondary aquatic feature. As shown in the first section of this paper (page 169ff.), the secondarily aquatic modifications of the urodeles involved the entire loss of the dermal skeleton, so far as the girdle is concerned. In the case of the superficial muscles attached to the suprascapula, the tendency to become membranous seems to be associated with this loss and is a further step in the same direction. (See discussion of serratus superficialis below.) As stated before, the skeleton of *Sphenodon* is more primitive, generally speaking, than that of *Megalobatrachus*, but the opposite of this is at times true regarding the musculature, which is often more generalized in *Megalobatrachus* than in *Sphenodon*, so far as the differentiation of the muscle masses is concerned, while the general status of their origin and insertion would tend to follow the trend of the skeleton, and would thus be nearer to the ancestral condition in *Sphenodon*. For example, the existence of a dermal clavicle in the latter is a survival from the stegocephalian condition. Hence the muscles attaching to it would necessarily show more primitive relations to the skeleton than in the case of the urodeles where the clavicle is lost and the musculature must find a secondary attachment on the underlying primary girdle elements.

In the restoration of the *Eryops* musculature, the levator scapulæ, therefore, is shown (Fig. 30) as a single muscle mass originating on the side of the pharynx and from the transverse processes of the anterior vertebræ, and as inserting along the anterior surface of the cleithrum as far as its junction with the clavicle. The *Eryops* scapula shows good opportunity for this insertion. The innervation may be assumed to be from the vagoaccessory nerve and from as many spinal nerves as would correspond with the number of transverse processes which may have shared in its origin.

Serratus Superficialis

Figures 29, 30

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> The only apparent homologue in this form is a tendinous sheet which arises from the superficial fascia of the lateral surface of the body wall posterior to the pectoral girdle	<i>Origin</i> As two fleshy slips from the distal ends of the last cervical and the first sternal rib (vertebral segments 8 and 9). These slips soon unite
<i>Insertion</i> By an insensible gradation into the cartilage of the posterior part of the suprascapula	<i>Insertion</i> As a single broad muscle on the medial surface of the posteroventral margin of the suprascapula and of the posterodorsal corner of the bony scapula
<i>Innervation</i>	<i>Innervation</i> Nn. thoracici superiores of the 8th spinal nerve and to a certain extent of the 7th and 9th spinal nerves

As above indicated, this muscle does not appear as a separately differentiated muscle in *Megalobatrachus*, as it does in *Sphenodon* (Fig. 29). In reptiles generally, the serratus superficialis is that muscle of the serratus system which originates on the ends of the last cervical and first thoracic ribs and inserts on the medial surface of the posterior border of the suprascapula and to a slight extent on the bony scapula. It is composed of more superficial fibres than the serratus profundus and inserts posteriorly to it. The serratus muscles of urodeles, as will be shown in the discussion of the serratus profundus, are more nearly comparable to the latter. In *Megalobatrachus* the posterior border of the suprascapula gradually attenuates into a connective tissue sheath occupying the superficial position of the serratus superficialis of *Sphenodon* and extending in the direction of the thoracic ribs beneath the latissimus dorsi. This may well represent a vestige of the serratus superficialis, common to the ancestors of reptiles and urodeles, which has disappeared as the result of lessened stress on the girdles due to aquatic adaptation.

It should, however, be considered an integral part of the general serratus system, which comprises superficially the fibres of the serratus superficialis, and more deeply the deeper fibres of the serratus profundus. This will be further discussed below.

As *Eryops* was a partially terrestrial animal, the stresses on the girdle, necessitated by dragging its considerable weight over the ground, would necessitate a well-developed serratus system, including a powerful serratus superficialis. As a variable origin of the two slips in *Sphenodon* is recorded (Fürbringer, 1900, p. 466, last cervical and first thoracic; Newman, 1877, p. 238, last two cervicals; Osawa, 1898, p. 553, first two thoracic ribs), it is apparent that they arise from the ribs most favorably situated with reference to the position of the suprascapula. In *Eryops* two ribs would be in this position. Hence it is probable that there were at least two slips for this muscle, inserting together into the posterior border of the heavy scapula as indicated in the inferred restoration (Fig. 30).

Serratus Profundus
Figures 28 to 32

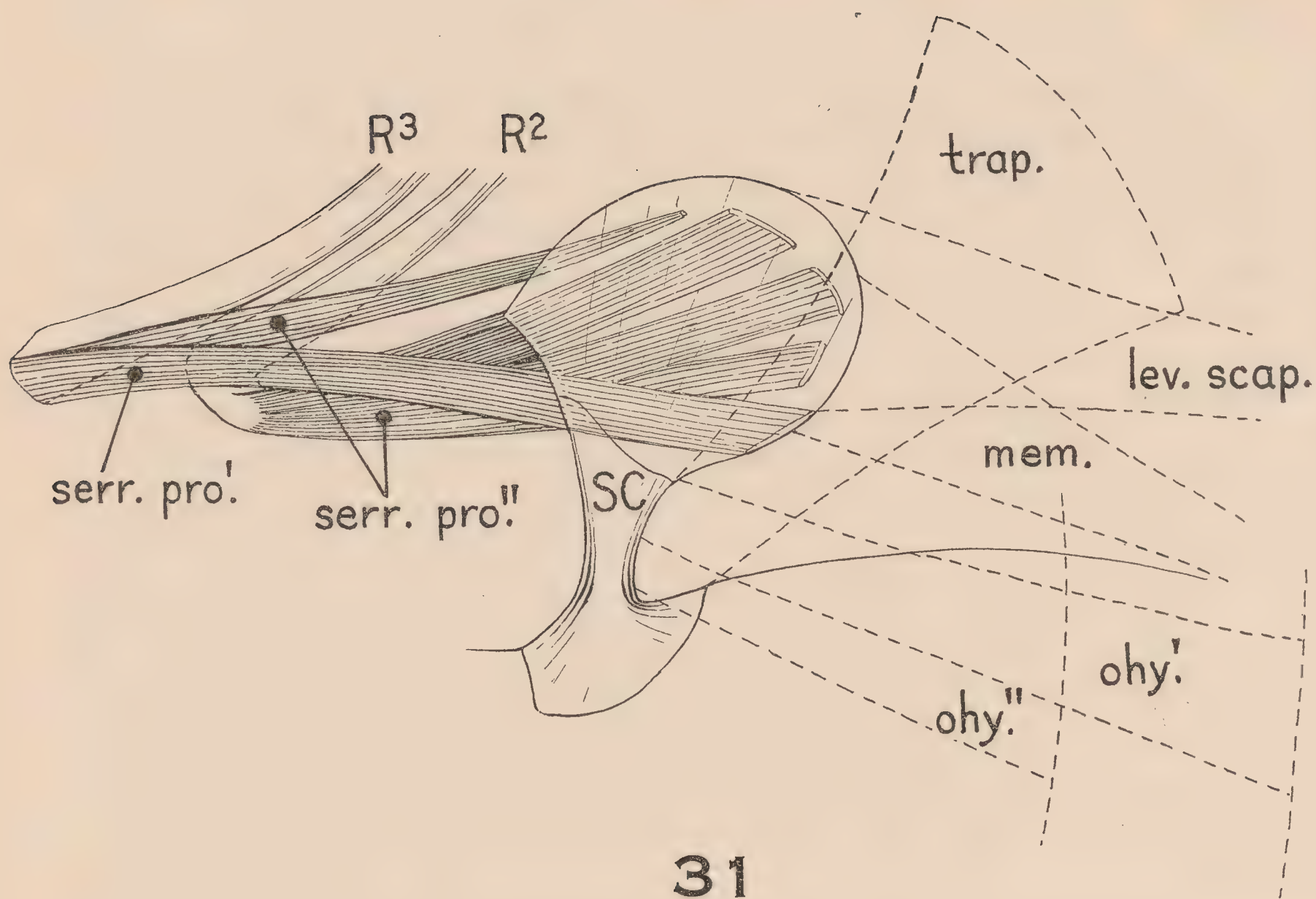
MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Superficial layer— Extremity of third rib Deeper layer— Extremities of second and third ribs; in latter case, immediately beneath origin of superficial layer	<i>Origin</i> Superficial layer— Extremities of third and fourth ribs Deeper layer— First to fifth ribs, i.e., all the cervical ribs, from above their extremities, the last from the region of the uncinat process
<i>Insertion</i> Superficial layer— Anteroventral border of supra- scapula on medial side near junc- tion with bony scapula as a single straight ribbonlike muscle Deeper layer— The slip from the third rib as a single tapering muscle with a nar- row insertion on the medial sur- face of the suprascapula near its posterodorsal border. The slip from the second rib is broad and separates to three equal parts, in- serting near the anterior and anterodorsal border of the supra- scapula on the medial surface	<i>Insertion</i> Superficial layer— As two separate straight ribbonlike muscles, on the anteromedial sur- face of the suprascapula ventral to the insertion of the deeper layer Deeper layer— The various slips partially unite to insert contiguously in a line along the dorsomedial border of the suprascapula throughout its whole extent. Anteriorly, the insertion is above that of the two slips of the superficial layer
<i>Innervation</i> N. spinalis III	<i>Innervation</i> Nn. spinales IV to VIII

This is variously named by Fürbringer, in the case of *Sphenodon*, levator scapulæ et serratus profundus and the collothoraciscapularis profundus, while Osawa makes the superficial and deeper layers two separate muscles under the names of serratus profundus and colloscapularis respectively. I agree with Fürbringer in considering them two layers of the same muscle, but both his names seem to me an unnecessary complication, as the various slips form the profound layer of the serratus system as compared with the serratus superficialis, and they are, therefore, more appropriately and more simply to be termed the serratus profundus, thus including under this name both the serratus profundus and colloscapularis of Osawa.

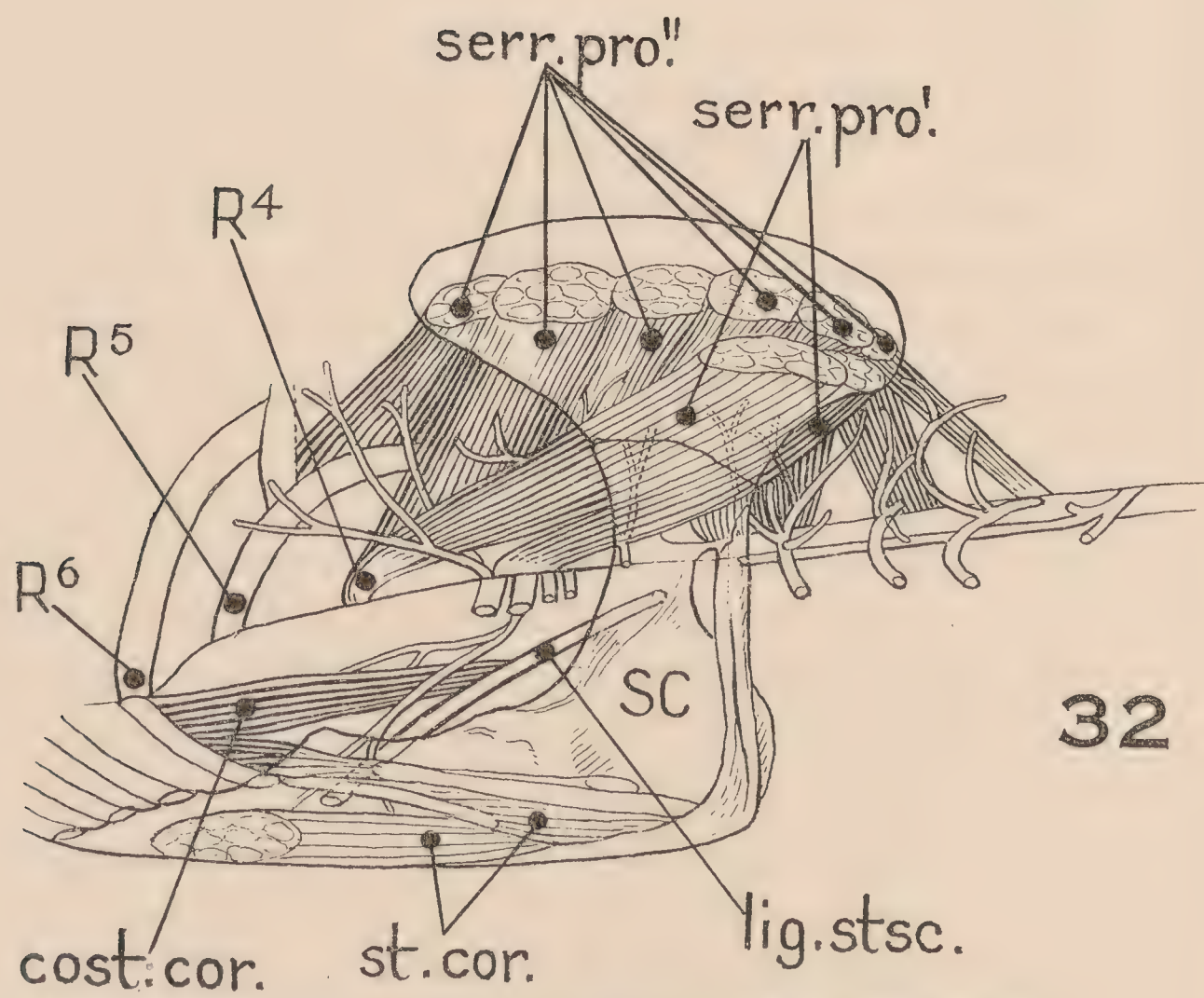
In *Megalobatrachus*, Osawa gives but one serratus muscle under the name of thoraciscapularis as equivalent to the serratus magnus of Humphry and Hoffman. This is evidently homologous to the serratus profundus of *Sphenodon* and not to the serratus superficialis, since the insertions of all the slips are on the dorso-anterior border of the suprascapula and not on the posterior border as in the case of the latter muscle.

Osawa mentions but one muscle here, originating from the point of the third rib as a single bundle and dividing to insert as three slips. My dissections (figures 28 and 31) show an origin from both the second and third ribs. The slip from the second rib divides into three slips as in the case of Osawa's muscle, only differing from it in the rib of origin. In addition, I find two other muscles arising from the third rib, overlapping at their origin. The inner muscle passes anterodorsally and parallel to the triple muscle from the second rib and inserts posteriorly to its most dorsal slip by means of a tapering point, as shown in the figure. The more superficially originating muscle passes straight anteriorly as a long band, and, crossing all three slips from the second rib on their superficial side, inserts ventrally to them on the lower anterior medial surface of the suprascapula, just above its junction with the bony scapula. This latter slip, as it is located more superficially than the others, appears to be homologous with the superficial part of the serratus profundus in *Sphenodon* (Fig. 32), while the remaining deeper slips are equivalent to the deeper layer in *Sphenodon*.

It might be suggested, in passing, that the single muscle arising from a rib and then separating into three slips may indicate three fused segments and also the phylogenetic dropping out of vertebræ. In *Sphenodon*, which in this respect may represent more nearly the ancestral condition, each slip of the same layer arises from a separate vertebral segment.



31



32

Fig. 31.—Dissection of the serratus profundus musculature of *Megalobatrachus*.

Fig. 32.—The serratus profundus system of *Sphenodon*, after Fürbringer.

As Osawa's observations on the specimens examined by him are without doubt accurate, there is apparently a considerable variation possible in this muscle. This also occurs in *Sphenodon* in the case of the serratus superficialis. While Fürbringer records it as arising from the fifth and sixth ribs, Newman records it from the fourth and fifth ribs, and Osawa from the sixth and seventh. Likewise, Fürbringer records the serratus profundus (my nomenclature) as arising in its superficial layers from the third and fourth, or second, third and fourth ribs, while Osawa records it from the fourth, fifth and sixth ribs. In the deeper layer there is a similar variation, while the innervation varies to correspond.

Since we may consider the reduced condition in *Megalobatrachus* as secondary, the serratus profundus of *Eryops* was nearer to the more typical arrangement seen in *Sphenodon*, though doubtless still more primitive in its segmental separation. The variation in the number of slips recorded within the same species, as exemplified in both *Sphenodon punctatus* and *Megalobatrachus japonicus*, on both the amphibian and reptilian lines, shows that this was always characteristic of the muscle and that it probably depends on the number of segments attracted into the anlage of the pectoral limb during the ontogeny of the individual, and their adaptive location with reference to the position of the scapular blade. In *Eryops*, four slips are shown in figure 30 posterior to the shoulder girdle, and doubtless a slip arose from each cervical rib as well.

The insertions of the serratus profundus in both *Sphenodon* and *Megalobatrachus* seem to follow the line on the under surface of the suprascapula of the primordial cleithrum, i.e., along the dorsal and anterior border. This may account for the presence of dermal cleithral-like bones in Anura, as shown by Schmalhausen (1917). Shann (1919, p. 536), has shown that in selachians the serratus muscle (retractor lateroventralis pectoralis) inserts as to its superficial fibres on the posterior border of the scapula, while a few deeper fibres insert on its inner surface. The former may be regarded as more or less equivalent to the serratus superficialis of reptiles and the latter to the serratus profundus. In Holocephali, he has shown (*loc. cit.*, p. 548) that this mass has separated into two distinct muscles, one of which inserts on the outer surface of the scapula and the other on the inner surface. In Chondrostei he finds (p. 556) that the entire muscle inserts on the inner side of the scapula, but that it does not reach the cleithrum, while, in the majority of the Teleostei (p. 560), it is attached to the upper portion of the cleithrum. In *Lophius*, however, the muscle is highly developed in correlation

with the mobility of the pectoral fin and is differentiated into five distinct slips, all of which insert at intervals along the inner side of the cleithrum.

From the above facts and from the condition of the insertion in amphibians and reptiles, it may be inferred

(1) That the serratus, both superficialis and profundus, originated as a series of segmental muscles arising from the septa and the ribs, strengthening them and inserting on the posterior and inner surface of the cartilaginous scapular bar of early sharks and ganoids;

(2) That, in the bony fishes, as the cartilaginous scapula became reduced and functionally replaced by the cleithrum, the serratus became attached to the cleithrum or lost;

(3) That, in the Stegocephalia and in the transitional types that led to them, there was a tendency for this muscle to divide into a more superficially located serratus superficialis, inserting on the posterior border of the scapula, and a deeper-lying serratus profundus, the fibres of which, in segmental bundles from the respective ribs, inserted on the upper and anterior part of the inner surface of the scapula where it was braced by the cleithrum. This is the condition adopted in the restoration of *Eryops*;

(4) That, in the reptiles, the cleithrum soon disappeared leaving the serratus profundus insertions to mark its former position, while the serratus superficialis was retained;

(5) That, in urodeles, the latter muscle disappeared as a result of aquatic life, leaving only a membranous fascia to mark its former position, while the former was retained as in reptiles, but with a lessened number of slips. In Anura, the same was true with regard to the serratus profundus, but the homologue of the serratus superficialis is, apparently, present and the cleithrum is often retained.

Omohyoideus and Sternohyoi-

deus (anterior part)

Omohyoideus

Figures 28 to 30, 33

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> As omohyoideus it arises from the anterior border of the bony scapula at junction with procoracoid	<i>Origin</i> Anterior border and inner face of the bony scapula and from the ligamentum sternoscapulare internum
<i>Insertion</i> Joins sternohyoideus as two slips, at first and second inscriptiones tendinei anterior to the heart. After this junction, the sternohyoideus runs anteriorly to insert on the ventral surface of the œsophagus and then on the copula and medial ends of the two branchial arches	<i>Insertion</i> On hyoid bone and its posterior process and on the second branchial arch
<i>Innervation</i> Sternohyoideus N. hypoglossus N. sternohyoidei Omohyoideus N. sternohyoideus N. supraclavicularis	<i>Innervation</i> N. hypoglossus Ramus ventralis of N. cervicalis I

As seen above, the omohyoideus of *Sphenodon* is homologous with the omohyoideus of *Megalobatrachus* plus the anterior part of the sternohyoideus. This is evident for the following reasons.

(1) Similar origin on the anterior border of the bony scapula. (But note the additional origin from the ligamentum sternoscapulare internum in *Sphenodon*.)

(2) Insertion on the two hyoid arches of the combined muscles in *Megalobatrachus*, which together have the same relations as the so-called omohyoideus of *Sphenodon*.

(3) Almost identical innervation in both cases, the hypoglossal nerve and the most anterior spinal nerves functioning in a similar way in both types. This innervation clearly interprets the muscle homology as above stated.

It is thus apparent that the omohyoideus may be regarded as the lateral slip of an original single anterior ventral muscle which arises from

the shoulder girdle, and, as will be shown below, from the sternum as well, and inserts typically on the hyoid arches. This lateral slip is thus separated only at its origin in *Megalobatrachus*, and throughout its entire extent in *Sphenodon*. It should be regarded as an integral part of a general ventral muscle system including also those treated immediately below.

Sternohyoideus
(posterior part)

Sternocoracoidei and
Costosternocoracoideus

Figure 33

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Posterior border of sternum just anterior to insertion of M. abdominis rectus	<i>Origin</i> Sternocoracoideus superficialis Inner surface of sternum following the labium internum sulci coracoidei and from first sternocostale Sternocoracoideus profundus Inner surface of posterior part of sternum Costosternocoracoideus Lateral half of first sternocostale
<i>Insertion</i> Joins omohyoideus and with it inserts on the two gill arches	<i>Insertion</i> Sternocoracoideus superficialis Inner surface of coracoid toward medial part Sternocoracoideus profundus By small tendon on sternocoracoidal border between sternocoracoideus superficialis and the costosterno- coracoideus Costosternocoracoideus On the ligamentum sternoscapulare internum
<i>Innervation</i> N. sternohyoideus N. rectus abdominis both from N. spinalis II	<i>Innervation</i> Sternocoracoidei Both from Nn. spinales VII, VIII and IX, but especially from VIII Costosternocoracoideus Nn. spinales VIII and IX

The sternocoracoidei and costosternocoracoideus muscles of *Sphenodon* (Fig. 33b) can best be explained as the remnants of a former

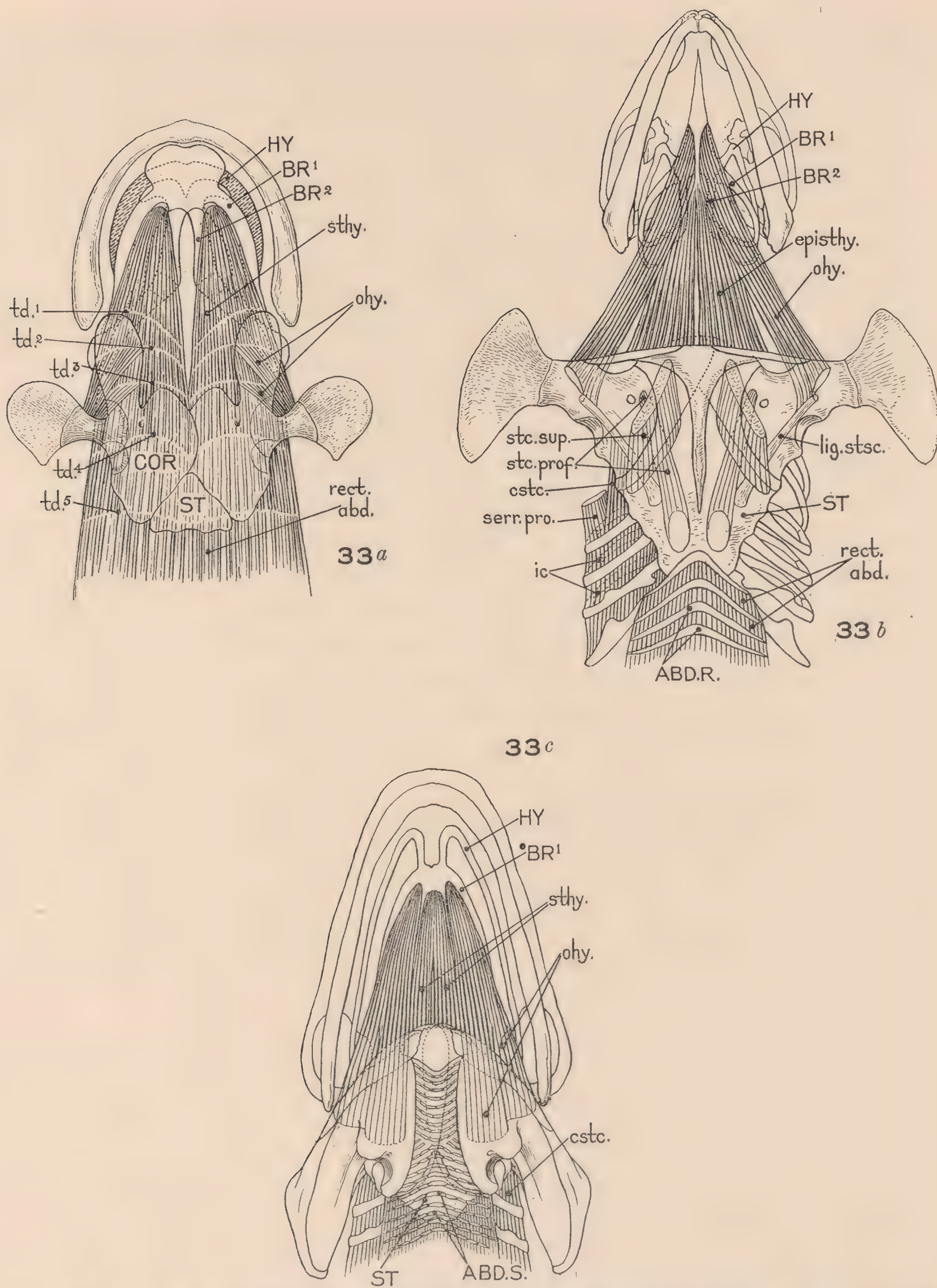


Fig. 33.—The ventral girdle musculature of *Megalobatrachus* (33a), *Sphenodon* (33b), compared, and the homologous musculature as inferred for *Eryops* (33c).

Note also the restoration of the cartilaginous epicoracoids, sternum, and the arrangement of the abdominal scutæ in *Eryops*. The shoulder girdle in each case is shown as if transparent.

sternohyoideus muscle as seen in its more primitive condition in *Megalobatrachus* (Fig. 33a). This view is strengthened by the following points.

(1) In both forms, these muscles arise wholly or in part from the interior surface of the sternum especially toward its posterior border.

(2) In *Megalobatrachus*, the sternohyoideus unites with the omohyoideus and, with it, inserts on the hyoid skeleton, while, during its course, it is crossed by a number of inscriptions tendineae, thus attesting its segmental nature. In *Sphenodon*, the outer slip, the costosternocoracoideus muscle, inserts on the posterior side of the ligamentum sternoscapulare internum, from the anterior side of which arises a part of the omohyoideus muscle which finally inserts on the hyoid skeleton. Both these muscles as part of the ventral system were originally segmental muscles, and the ligament above mentioned may be interpreted as equivalent to a fusion of tendinous myocommata of the original segments. As shown by Romer (1922, p. 547), in the fishes and lower vertebrates this was expressed by the mesocoracoid arch (supraglenoid buttress). In *Sphenodon* and lizards generally, this became reduced to a ligament, while, under the view here presented, in the aquatic urodeles, as represented by *Megalobatrachus*, it became still further reduced as an aquatic adaptation along with many other features of the skeleton. In *Megalobatrachus*, as shown on page 168 and in figure 13a of this paper, there is a structure which may be a reduced supraglenoid buttress, but in most urodeles there is apparently no indication of it, except in so far as the tendinea scripta of the muscle may be regarded as homologous in part.

(3) The fact that the sternocoracoidei in *Sphenodon* have short courses and insert on the coracoid may be explained by regarding them as segmental units of a former sternohyoideus, the anterior segments of which are represented by the episternohyoideus.

(4) The posterior relations of the origin of the sternocoracoidei to the abdominis rectus parallel the similar relations in *Megalobatrachus* of the origin of the sternohyoideus to the insertion of the abdominis rectus in that form. It is evident from the innervation and these relations that the whole anterior ventral system is a continuation of the general rectus abdominis musculature in both *Sphenodon* and *Megalobatrachus*.

As applied to *Eryops* (Fig. 33c), the inference would be that the abdominis rectus inserted on the posterior border of a cartilaginous sternum. From this point forward, it was in practical continuation with a sternohyoid segment which in turn passed anteriorly internal to the median cartilaginous extensions of the coracoids to insert on the inner face of the interclavicle which interrupted its continuity with the

episternohyoid. The latter in turn inserted on cartilaginous hyoid arches similar to those of *Megalobatrachus*. The lateral portions of this anterior muscle mass arose from the M. abdominis rectus laterally, or from the first sternocostal cartilages, and passed forward with the sternohyoid to insert on the posterior edge of the mesocoracoid (supraglenoid) buttress, while from the anterior edge of the latter, and from the inner face and lower anterior angle of the scapular border, the omohyoid passed forward laterally to the sterno- and episternohyoid to insert also on the hyoid apparatus. It is suggested that this whole muscle mass was crossed at intervals by myocommata, and formed a unified system. The ventral scutes were arranged along the myocommata ventral to the ribs and with them converged to support the sternal apparatus ventrally, just as they overlap the posterior part of it in *Sphenodon*.

While much of this arrangement is necessarily conjectural because of the extent of the cartilaginous restoration, there are many indications that suggest its accuracy along broad lines.

The weight of the internal organs would require the efficient support of a cartilaginous ventral skeleton, which could have been formed only on the suggested lines, while the efficient bracing of the heavy, bony scapulocoracoid would require a powerful opposing pull on opposite sides of the mesocoracoid buttress.

B. VENTRAL MUSCULATURE FROM SHOULDER GIRDLE TO ARM, AND ON UPPER ARM

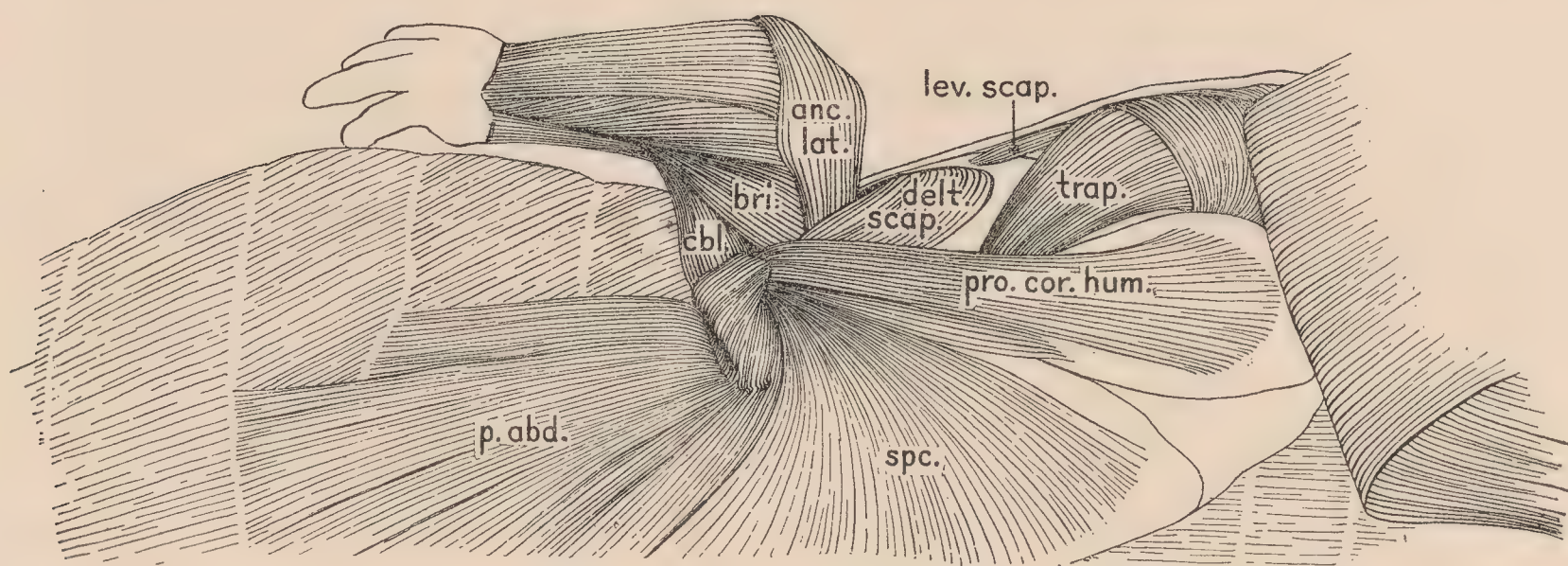
Pectoralis

Figures 19, 34 to 38

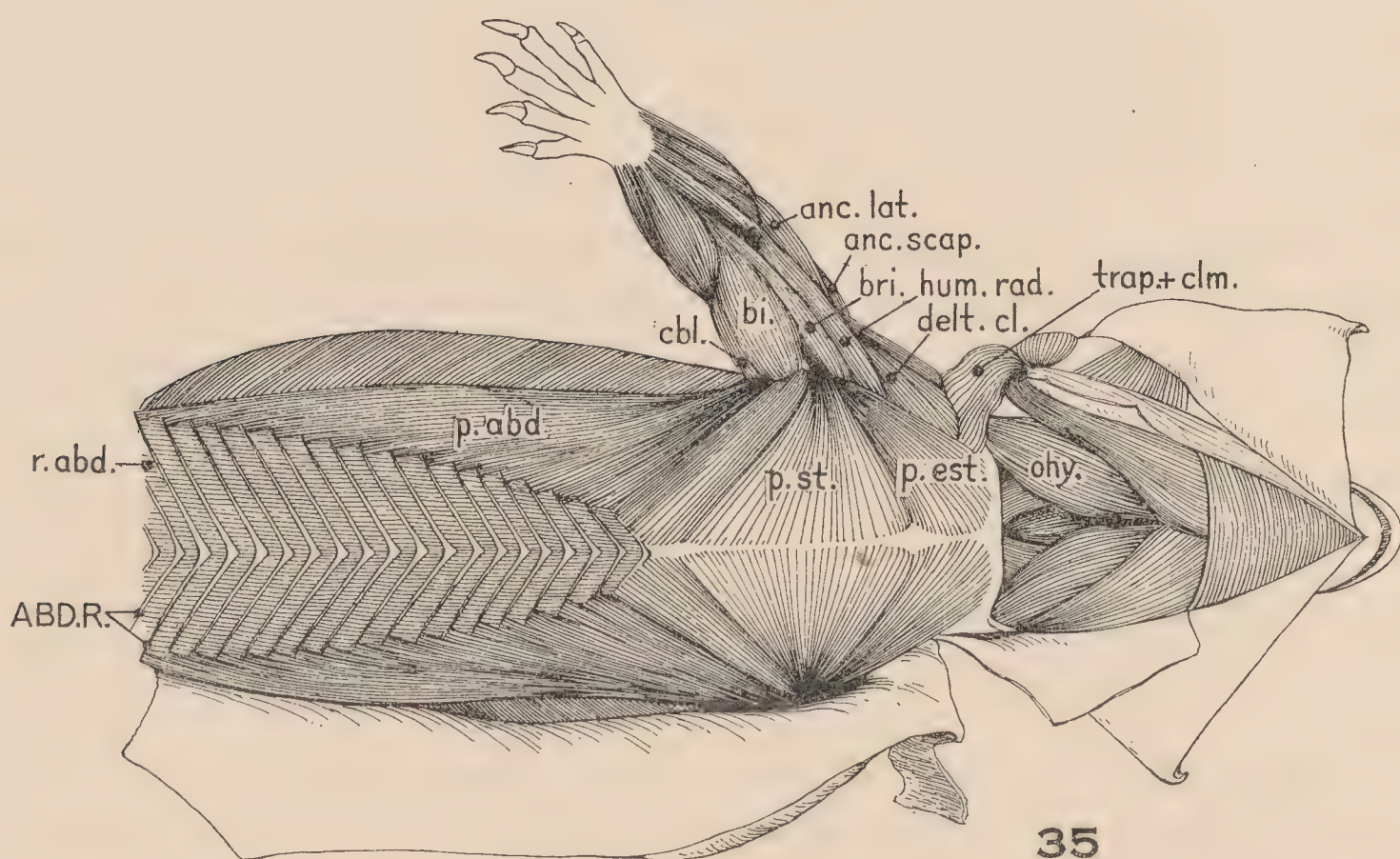
MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Outer surface of the sternum and 2d and 3d myocommata of the rectus abdominis	<i>Origin</i> Outer surface of clavicle, episternum, sternum and ends of ventral ribs
<i>Insertion</i> Converges to processus ventralis humeri just posterior to M. supracoracoideus	<i>Insertion</i> Converges to processus ventralis humeri posterior to M. supracoracoideus
<i>Innervation</i> N. pectoralis from N. brachialis longus inferior	<i>Innervation</i> N. pectoralis from N. brachialis longus inferior

The pectoralis is the most superficial portion of the ventral or flexor system of muscles which arises on the chest region and typically

inserts on the upper arm. Its superficial character is indicated not only by its position with reference to the other muscles of the system, but also by its origin from the dermal bone elements of the ventral part of the



34



35

Fig. 34.—Dissection of the superficial ventral musculature of the pectoral limb of *Megalobatrachus*.

Fig. 35.—Dissection of the superficial ventral musculature of the pectoral limb and throat region of *Sphenodon*.

girdle, and by its insertion on the most superficial part of the most prominent and most proximally situated bony protuberance of the forearm, the processus ventralis humeri, or deltopectoral crest.

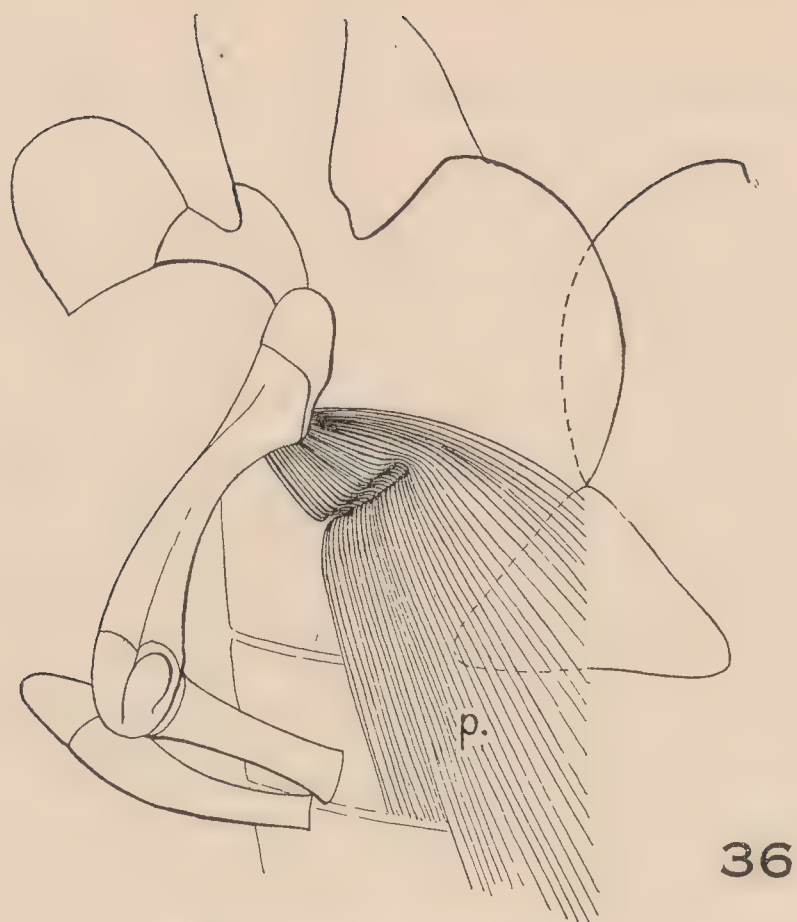
In both reptiles and urodeles, this muscle is seen to vary with the ventral dermal elements of the girdles with whose fortunes its history is

linked. This is clearly brought out by a comparison of the conditions in *Megalobatrachus* and *Sphenodon* as typical of these two groups.

In *Sphenodon* (Figs. 35, 37), where the ventral dermal elements are particularly complete, the main divisions of the muscle arise respectively from the clavicle, interclavicle, episternum, sternum and ends of the abdominal or ventral ribs, all of which parts, except the sternum, are dermal bones. In *Megalobatrachus* (Figs. 34, 36), on the other hand, in which the clavicle and interclavicle are wholly lacking, the origin of the pectoralis is confined to the sternum, represented only by a cartilaginous plate and the first two myocommata of the rectus abdominis, as indicating vestigially the course along which the ventral scutes were arranged in the stegocephalian ancestors.

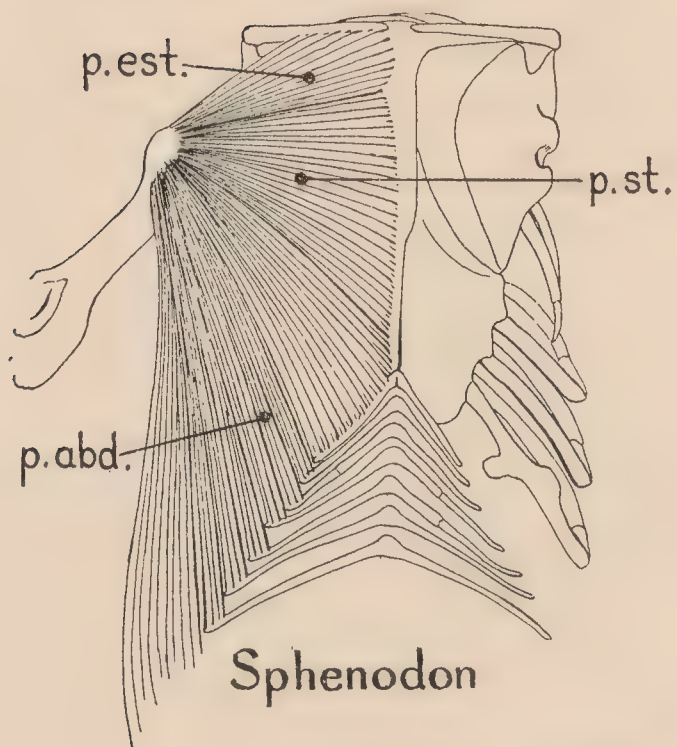
But *Eryops* had bony ventral scutes of dermal origin which were arranged in parallel rows much as in *Archegosaurus* (Fig. 5), its near relative. These must have supported the sternal plate ventrally, overlapping it as in the homologous dermal ventral ribs of *Sphenodon*, but to a much greater extent (Figs. 15, 38). When the dermal skeleton disappeared in the ancestral urodeles as an aquatic adaptation, the cartilaginous sternum was left behind, while the only representatives of the dermal ventral ribs and the cartilaginous pectoral ribs are the membranous myocommata. Hence, the pectoralis abdominalis of urodeles arises from the latter and the pectoralis sternalis from the former. There are no interclavicular or clavicular pectoral slips present, partly because of the total disappearance of these parts of the dermal girdle, partly because of the lack of underlying cartilaginous parts to take their place, and partly because of the great expansion of the supracoracoideus muscle which functionally has taken the place of the anterior slips of the pectoralis in the urodele group.

As will be obvious from the above, *Eryops* would more nearly resemble *Sphenodon* in respect to the pectoralis musculature, because of the presence of the primitive dermal skeleton. The weight of the animal also presupposes a powerful pectoral system. Hence, as shown in figure 38, all four slips of this muscle are inferred arising respectively from the clavicle, interclavicle, the interclavicular and sternal ventral scutes (inferred from the conditions in *Archegosaurus*), and from the abdominal armature of dermal scutes of which there are abundant remains in the fossil skeleton.



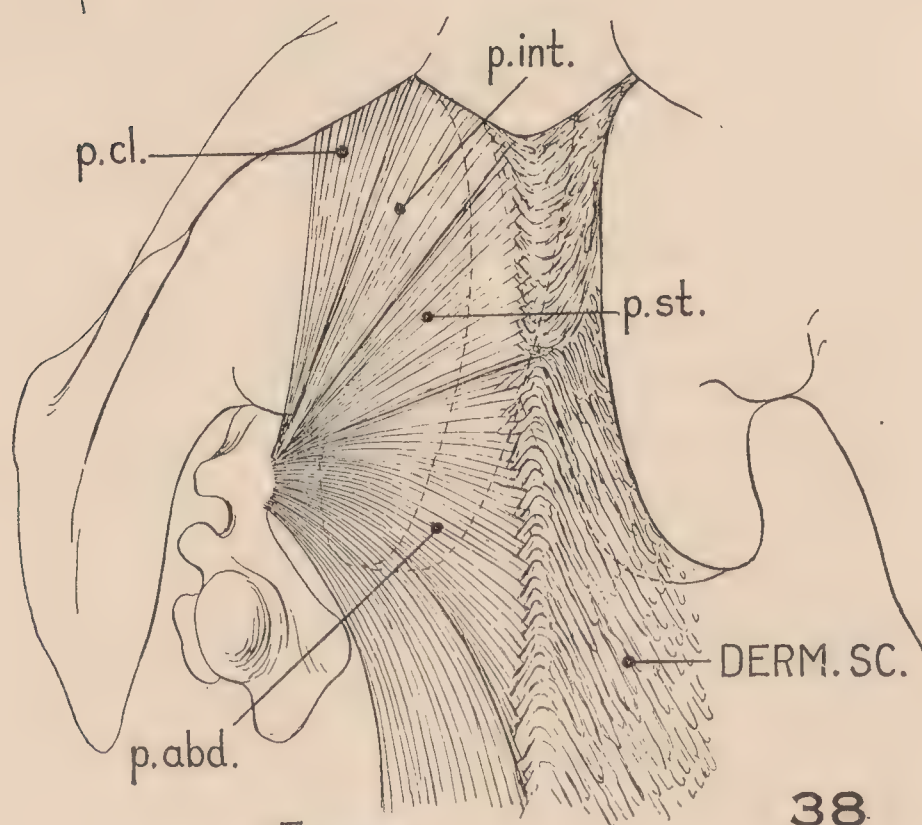
36

Megalobatrachus



37

Sphenodon



38

Eryops

Figs. 36, 37, 38.—Comparison of the pectoral muscle in *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*.

Supracoracoideus

Figures 19, 34, 39 to 43

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Outer surface of coracoid leaving its border free. Also slips arise from medial border of procoracoid and from membrane between it and coracoid. The most lateral of these slips, however, arising from center of procoracoid not homologous with supracoracoid of <i>Sphenodon</i>. (See scapulohumeralis)	<i>Origin</i> Anterior half of outer surface of coracoid except part bordering on scapula
<i>Insertion</i> Processus ventralis humeri between procoracohumeralis and pectoralis and part of humerus head anterior to it as well as part of capsule	<i>Insertion</i> Processus lateralis humeri between deltoides clavicularis and pectoralis
<i>Innervation</i> N. supracoracoideus from first spinal nerve entering plexus	<i>Innervation</i> N. supracoracoideus from first spinal nerve entering plexus

In *Megalobatrachus* (Figs. 34, 39, 41), this muscle covers the entire coracoid except its extreme border. It also has anterolateral slips arising from the membrane between the coracoid and procoracoid and from the medial border of the procoracoid. Another slip, however, arising from the center of the procoracoid underneath the M. procoracohumeralis, appears to be a deeper layer of the latter muscle, for both have an axillary innervation. It appears, therefore (Fig. 58), to be homologous to the scapulohumeralis muscle of *Sphenodon* and to the axillary innervated part of the acromiohumeralis of Anura, while the slip of the supracoracoideus arising from the medial border of the procoracoid corresponds to that part of the acromiohumeralis having a supracoracoid innervation (Cf. Anthony and Vallois, 1914, p. 251).

In *Sphenodon* (Figs. 40, 42), the supracoracoideus arises from the anterior half only, excluding also the part bordering on the scapula, from which originates the M. scapulohumeralis anterior. The latter occupies the same position and has the innervation of the lateralmost slip in *Megalobatrachus* as mentioned above and is therefore to be considered homologous with it.

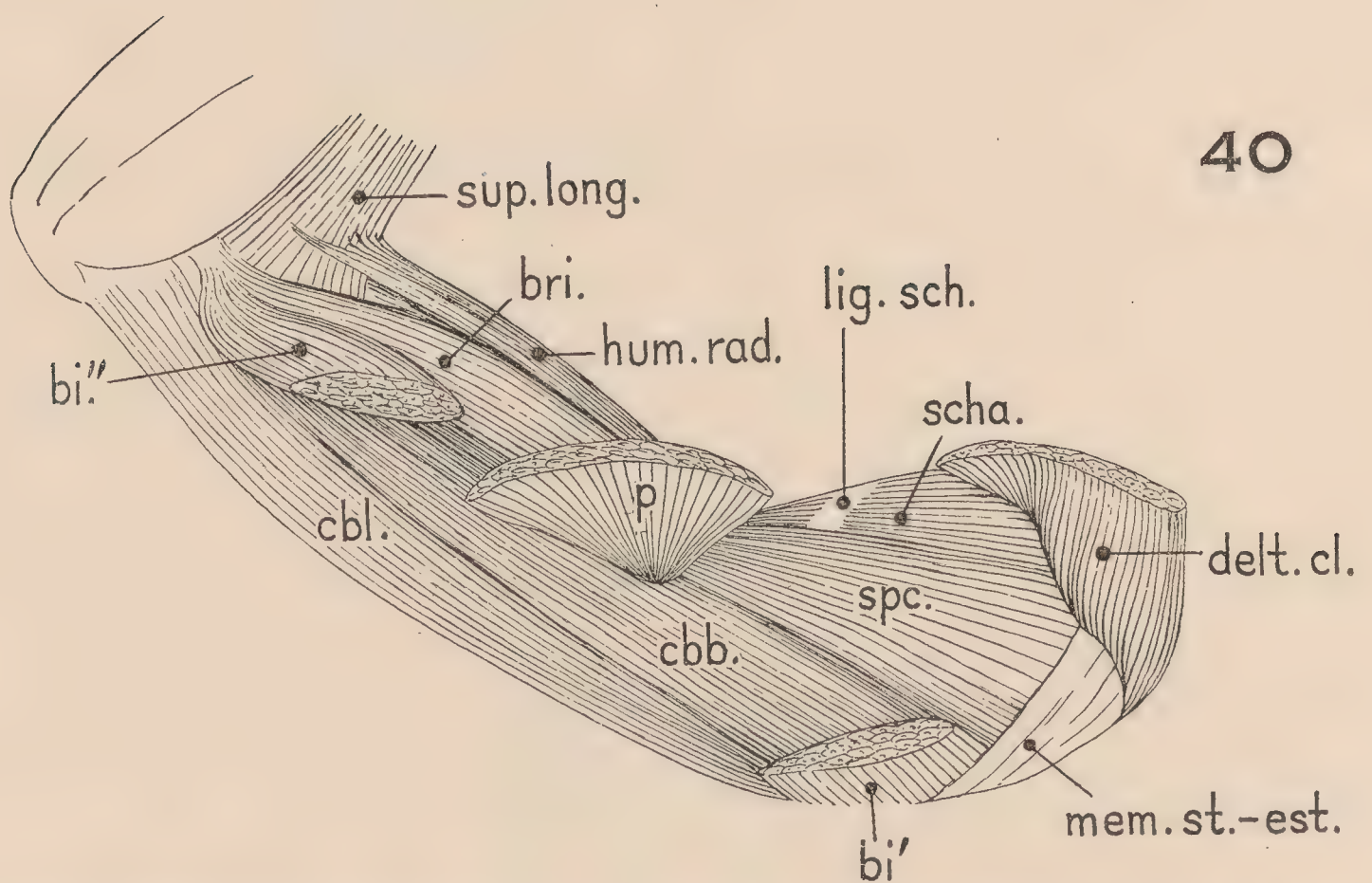
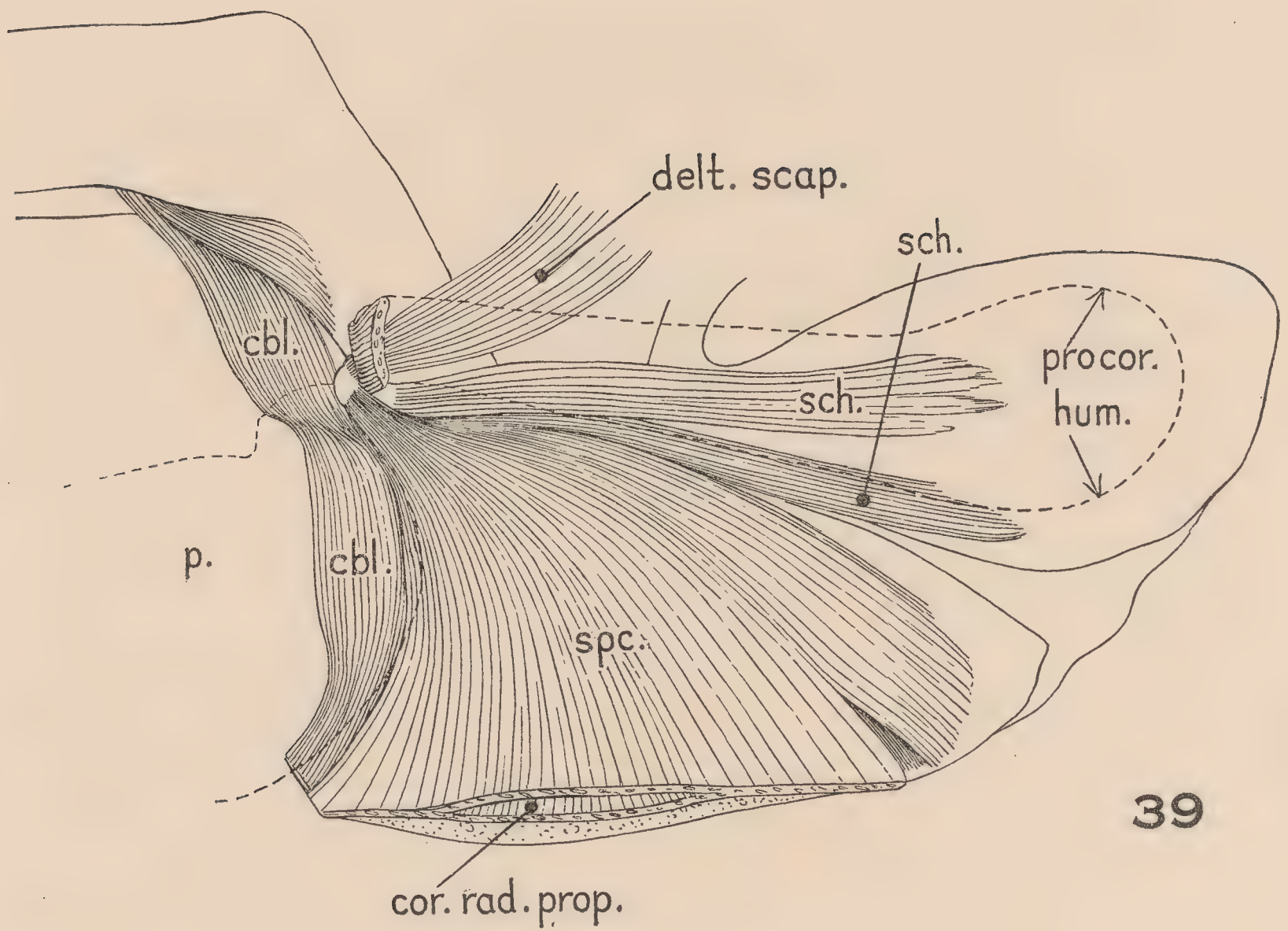


Fig. 39.—Dissection of the supracoracoid and neighboring musculature of *Megalobatrachus*.

Fig. 40.—Dissection of the supracoracoid and neighboring musculature of *Sphenodon*.

The supracoracoid proper is clearly homologous with the main portion of that muscle in *Megalobatrachus*, though it is confined to the anterior half of the coracoid by the encroachment of the coracobrachialis system on the caudal part of the latter. In *Megalobatrachus*, the M. coracobrachialis brevis arises from the caudal part but is overlapped by the posterior part of the supracoracoid-coracoradialis mass, while the coracobrachialis longus is confined to the posterior border of the coracoid.

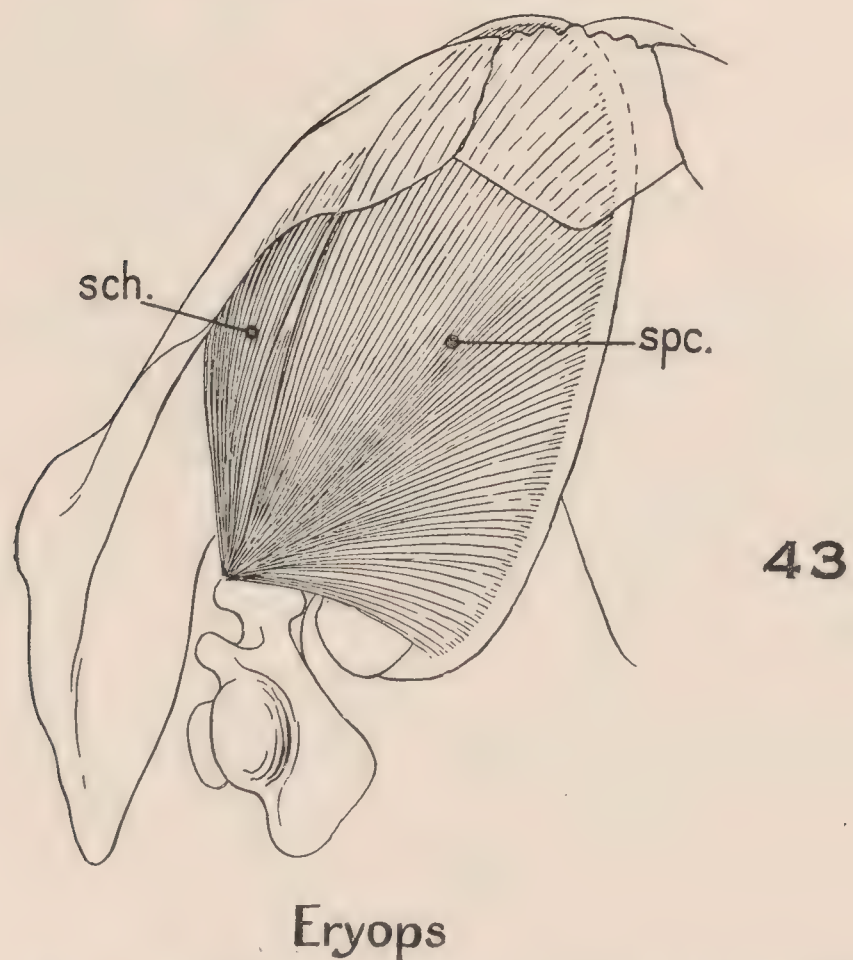
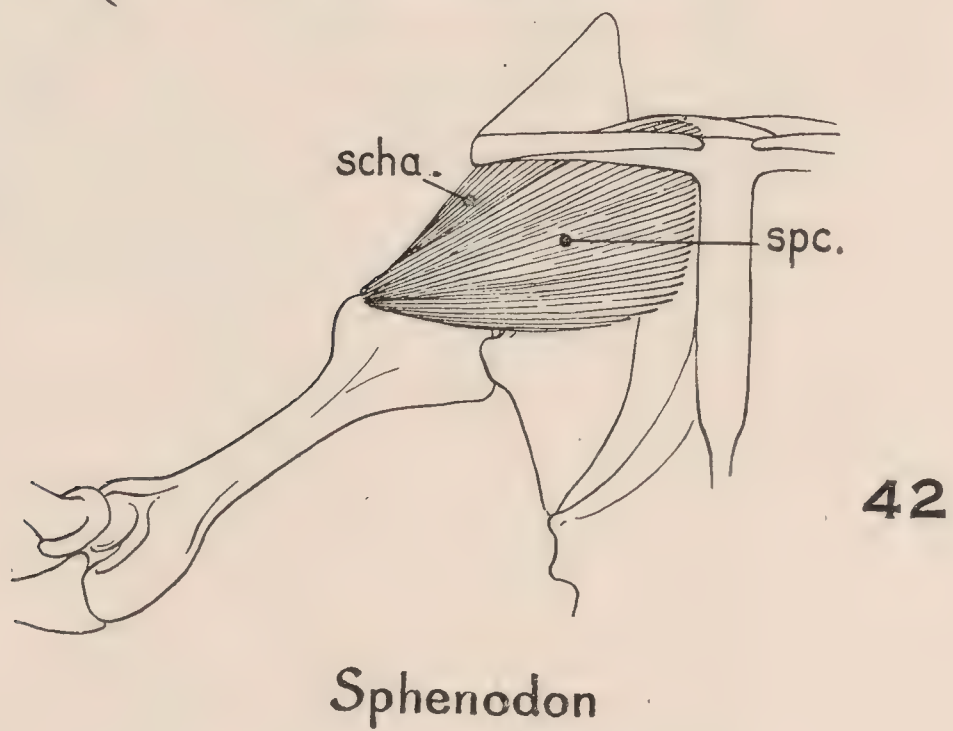
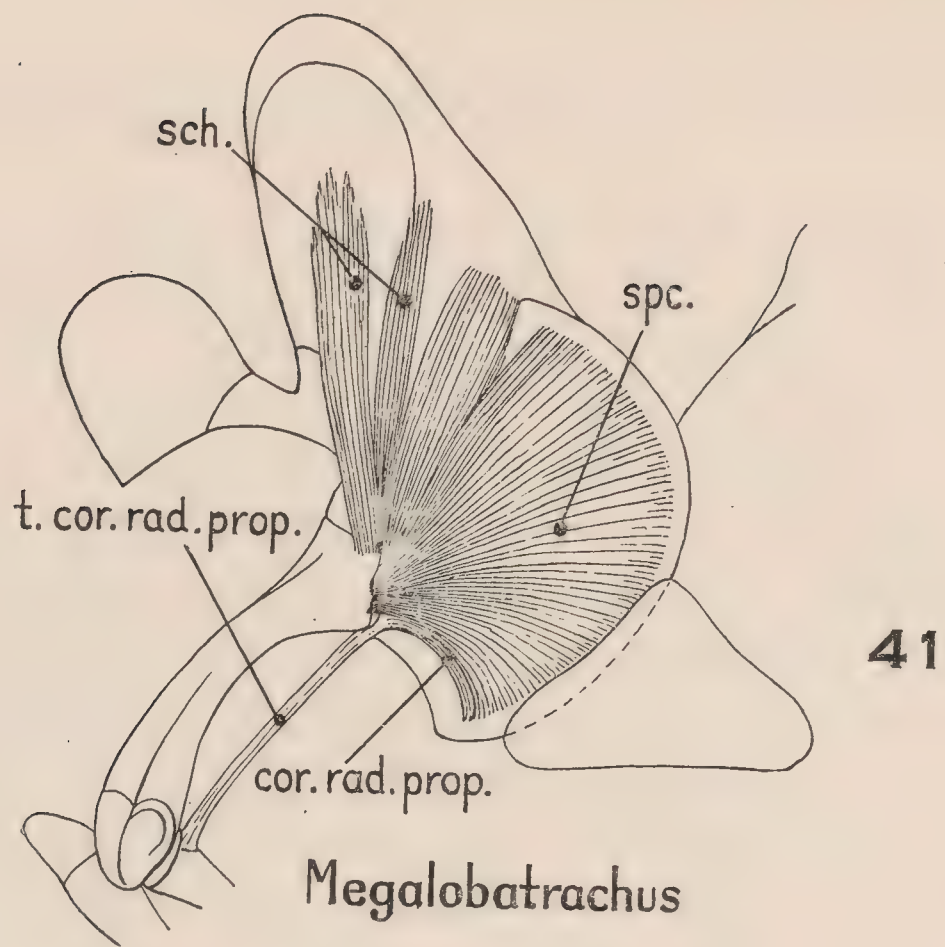
That the supracoracoid is not related to the pectoralis system, or to the coracobrachialis, as Romer suggests (1922, p. 533), is shown by the remoteness of their respective innervations, the former arising from the anterior border of the plexus, in fact hardly uniting with it, while the latter is from N. brachialis longus inferior. The supracoracoid nerve as judged by its anterior situation and interzonal course, together with its muscle, probably represents an anterior myotomic segment, while the pectoralis muscle with its nerve represents a following segment or perhaps more than one. Both the supracoracoid and pectoralis nerves are ventral and follow approximately parallel courses, except that the former passes through the girdle and the latter behind it. Again, the supracoracoid and pectoralis muscles follow each other in segmental fashion on the ventral side of the girdle, though the former overlaps the latter anteriorly. Again, the former inserts on the anterior side of the processus lateralis humeri and the latter on the lateral and posterior surface.

As the supracoracoideus exists in both amphibians and reptiles, it must have existed in the Stegocephalia, and is represented in the restoration of *Eryops* (Fig. 43) as arising from the cartilaginous part of the coracoid portion of the girdle throughout practically its whole extent.

Coracoradialis Proprius

Figures 39, 44, 46

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> In common with and as a deeper layer of M. supracoracoideus, separate in its posterior two-thirds	<i>Origin</i> Not present as a separate muscle. The deeper fibers of the supracoracoideus are probably homologous with it
<i>Insertion</i> Converges to a long tendon which gives off a slip to the processus ventralis humeri and inserts principally on head of radius above M. brachialis inferior	<i>Insertion</i> No tendon present as such, but this may be partly homologous to tendinous part of biceps brachii in <i>Sphenodon</i> (q.v.)
<i>Innervation</i> N. supracoracoideus	<i>Innervation</i>



Figs. 41, 42, 43.—Comparison of the supra-coracoideus and scapulohumeralis anterior musculature of *Megalobatrachus* and *Sphenodon* and their inferred restoration in *Eryops*.

This muscle is characteristic of Amphibia generally but is not found in reptiles, where it is functionally replaced by the *M. biceps brachii*. The innervation is from a branch of the *N. supracoracoideus* and is formed as a deeper layer of that muscle, being separated from it only

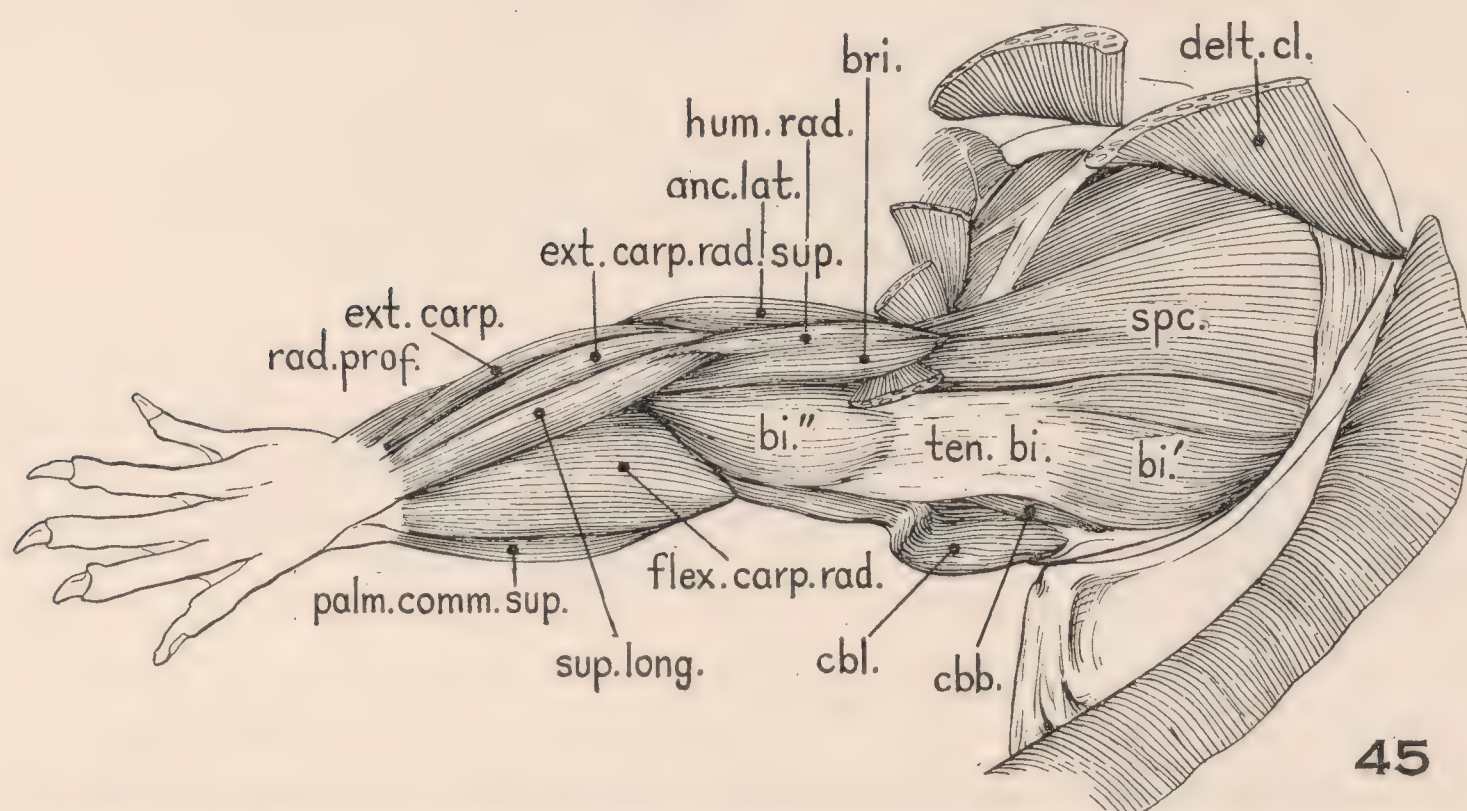
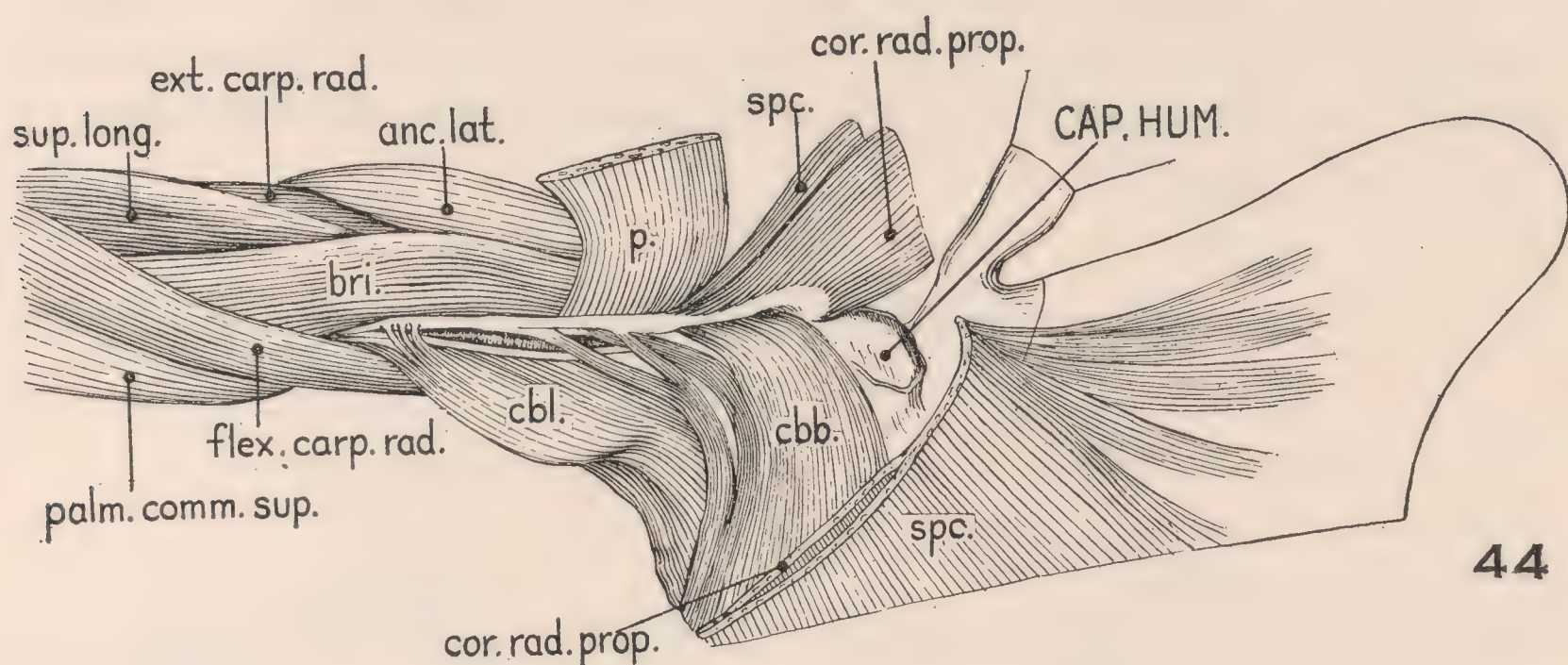


Fig. 44.—Dissection of the ventral upper arm musculature of *Megalobatrachus* with especial reference to the relations of the coracobrachialis proprius to the surrounding muscles.

Fig. 45.—Dissection of the ventral arm musculature of *Sphenodon* with especial reference to the biceps muscle.

caudally (Figs. 44, 46). It converges rapidly to a tendon on which it inserts, and through which it attains an insertion on the proximal part of the radius just beneath its head. This tendon apparently is derived from the membrana intermuscularis and separated off from it through the mechanical pull of the muscular mass of the coracoradialis proper.

While there is nothing equivalent to this as an independent muscle in *Sphenodon*, the deeper part of the supracoracoid in the latter may be taken as homologous with the muscular portion of the coracoradialis proprius of Amphibia.

This muscle probably did not exist in *Eryops* (Fig. 48), since it seems to be a secondary feature brought about by the attenuation of a primitive stegocephalian biceps, as explained under the discussion of that muscle (page 225).

Coracobrachialis Brevis

Figures 19, 40, 44 to 48

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Outer surface of caudal part of coracoid near posterior border beneath M. coracoradialis proprius	<i>Origin</i> Outer surface of posterior half of coracoid anterior to origin of M. coracobrachialis longus and lateral to that of M. biceps
<i>Insertion</i> On proximal end of humerus on medial side of processus ventralis humeri and by several strands on proximal part of tendon of coracoradialis proprius	<i>Insertion</i> Flexor surface of humerus between processus lateralis and medialis
<i>Innervation</i> N. coracobrachialis as for M. coracobrachialis longus	<i>Innervation</i> N. coracobrachialis as for M. coracobrachialis longus

This muscle should be considered as the deeper portion of the pectoralis system because of its closely related innervation, because of the general position of its origin caudal to the supracoracoideus system and because of the insertion of its main mass practically beneath that of the pectoralis insertion. In *Megalobatrachus* certain posterior fibres insert on the tendon of M. coracoradialis proprius. Their bearing on the homologies of the M. biceps brachii is discussed below under the heading of that muscle. In this same connection the contiguity of its origin in *Sphenodon* to that of M. biceps brachii should be noted.

The muscle is clearly recognizable in both reptiles and urodeles as homologous. It is evident that it occupied a similar position in *Eryops*.

Coracobrachialis Longus
Figures 19, 34, 35, 39, 40, 44 to 48

MEGALOBATRACHUS	SPHENODON
<i>Origin</i>	<i>Origin</i>
Caudal border of coracoid medial to origin of M. anconæus coracoideus	Posterior corner of coracoid medial to origin of M. anconæus coracoideus
<i>Insertion</i>	<i>Insertion</i>
Main mass of muscle splits to insert along the distal half of the antero-medial surface of the humerus by two fleshy bundles. Some fibres insert on the tendon of M. coracoradialis proprius	Distal part of medial surface of the humerus
<i>Innervation</i>	<i>Innervation</i>
N. coracobrachialis arising in common with N. pectoralis from N. brachialis longus inferior by three separate branchlets	N. coracobrachialis plus biceps arising in common with N. pectoralis from N. brachialis longus inferior, together with a series of more distal branches from the lateral branch of the latter

The fibres of this muscle arise in continuity with those of the preceding muscle from the posterior border of the coracoid in *Megalobatrachus* (Figs. 44, 46), and from the posterior surface of that region in *Sphenodon* (Figs. 45, 47), practically forming its most posterior mass.

It is much longer than M. coracobrachialis brevis, however, and inserts along the flexor surface of the humerus, a few fibres uniting with the posterior part of the tendon of the M. coracoradialis proprius in *Megalobatrachus*. The significance of these is discussed in connection with the discussion of the M. biceps brachii.

The innervation is the same as that of M. coracobrachialis brevis, together with which it forms a part of the pectoralis system.

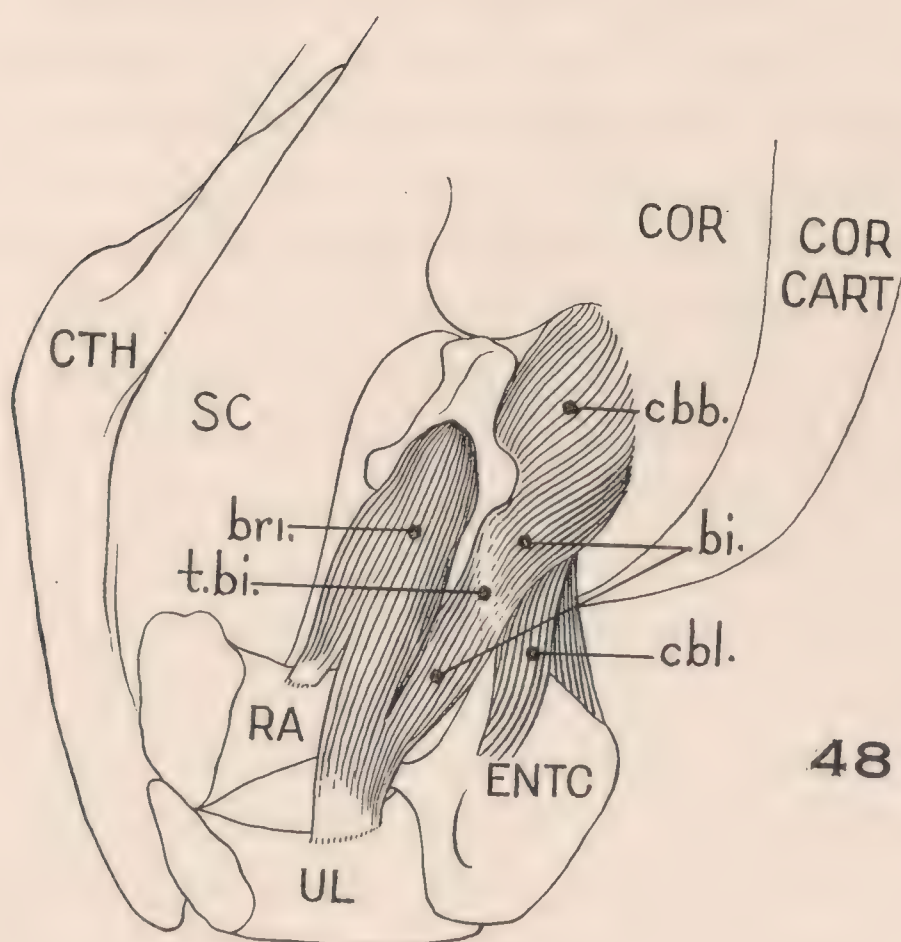
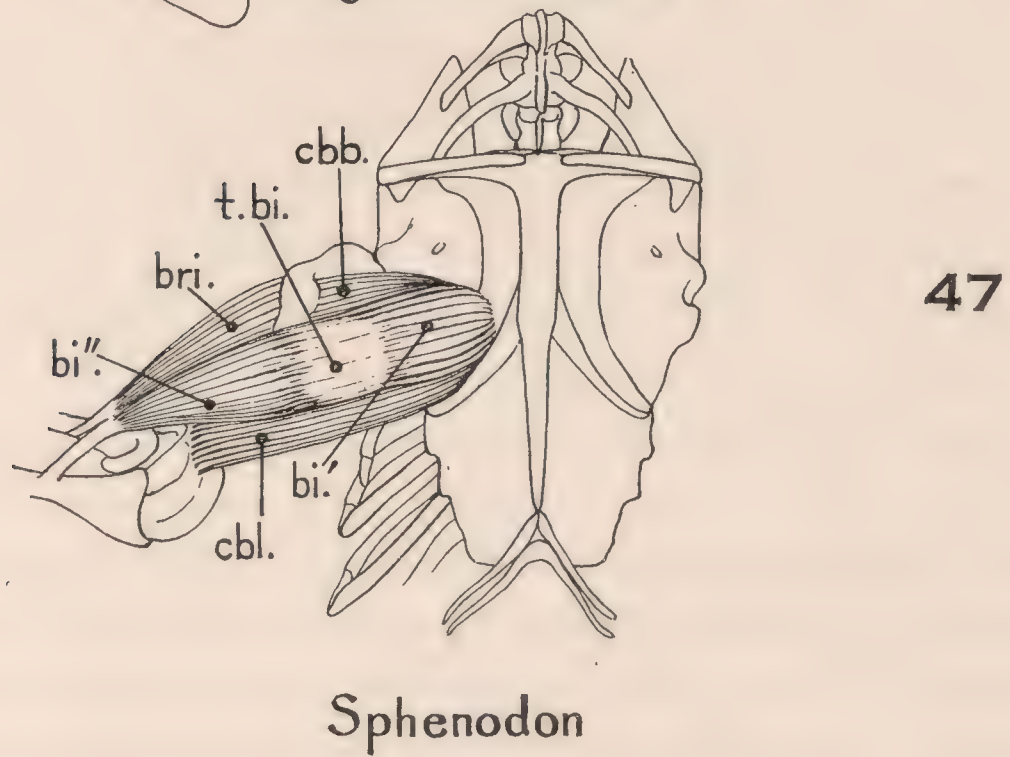
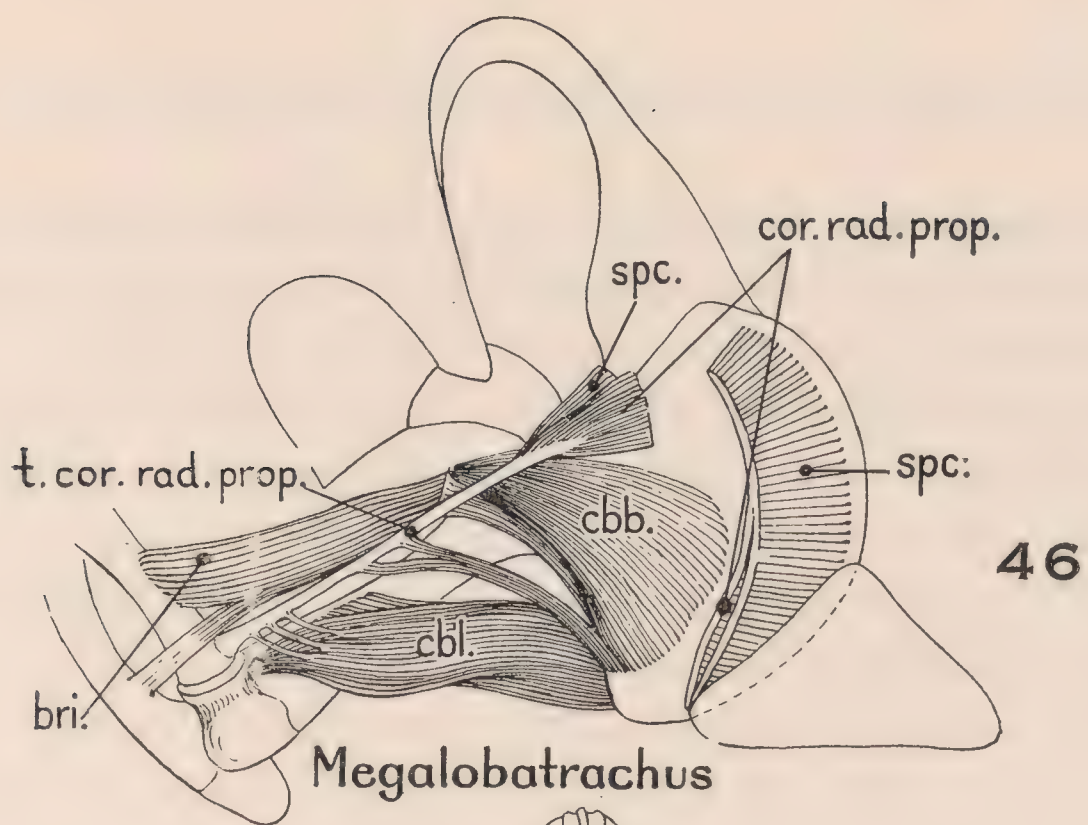
It bears practically the same relations in *Megalobatrachus* and *Sphenodon* and the homology is clear. In *Eryops* (Fig. 48) it was present under practically the same circumstances, but, owing to the shortness of the humerus shaft, was probably scarcely to be separated from the mass of coracobrachialis brevis. It arose from the posterior part of the coracoid and inserted on the anterior margin of the broadly expanded entepicondyle.

Biceps Brachii (Coracoantibrachialis)

Figures 19, 35, 40, 45, 47, 48

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Non-existent as biceps brachii, but perhaps equivalent at its origin to strands of M. coracobrachialis brevis which insert on tendon of M. coracoradialis proprius	<i>Origin</i> Medial border of coracoid caudal to M. supracoracoideus and medial to coracobrachialis brevis. The proximal portion passing from a fleshy muscular belly to a flat tendinous portion over the capsule of the joint. The latter is perhaps homologous in part to the tendon of the amphibian M. coracoradialis proprius
<i>Insertion</i> The posterior part of M. coracobrachialis longus splits off several strands that insert on the distal part of the tendon of M. coracoradialis proprius, which then inserts on the proximal end of the radius in close proximity to the insertion of M. brachialis inferior, which latter also inserts by a tendinous slip on the proximal part of the ulna. This arrangement is generally similar to that of the distal belly and insertion of M. biceps brachii in <i>Sphenodon</i>	<i>Insertion</i> The above tendon becomes a distal fleshy belly occupying the distal part of the flexor surface of the humerus symmetrically placed beside the M. brachialis inferior, with which it unites distally to insert by a double tendon on the proximal end of the radius and ulna and on the elbow-capsule
<i>Innervation</i> Both muscles are innervated by Nn. coracobrachiales from the trunk of N. pectoralis and finer branchlets from N. brachialis longus inferior	<i>Innervation</i> Proximal belly innervated by N. coracobrachialis plus biceps from main trunk of N. brachialis longus inferior in close proximity to N. pectoralis Distal belly innervated by Nn. coracobrachiales plus biceps from N. brachialis longus inferior lateralis which is the lateral continuation of the above trunk

The M. biceps brachii does not properly exist in amphibians, its place being taken functionally by the M. coracoradialis proprius. It is represented in a generalized condition in *Sphenodon*, where it is typical



Figs. 46, 47, 48.—Comparison of the humeroflexor musculature of *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*.

of the same muscle in reptiles and mammals. There are, however, certain homologies in *Megalobatrachus* which throw light on its origin and relations to other muscles.

In *Sphenodon* (Figs. 45, 47) it has two muscular regions, consisting of a proximal and a distal belly connected in the neighborhood of the processus lateralis humeri by a broad tendinous band. The proximal belly arises from the posterior part of the coracoid medial to, and in close proximity with the origin of the M. coracobrachialis brevis with which it shares the innervation, and with which it must be regarded as genetically connected. It inserts, as above mentioned, on a broad tendon which pulls freely over the joint of the humerus and in turn forms the origin of the posterior belly, innervated by the same nerve as the M. coracobrachialis longus but from more distally situated branches than those supplying brevis and the proximal belly of the biceps. It is also situated parallel to coracobrachialis longus throughout its course, the latter bounding it on the ulnar side. This distal belly, in turn, unites finally with the terminal portion of the M. brachialis inferior which bounds it radially and, together with it, inserts by means of a double tendon on the proximal part of the radius and ulna. It seems likely that this distal belly of the biceps has been formed by the union of fibres from both Mm. brachialis inferior and coracobrachialis longus.

In *Megalobatrachus* (Fig. 46) corresponding features are represented, but in rudimentary condition. Slips from the posterior part of the M. coracobrachialis brevis insert on a tendon, that with which the coracoradialis proprius unites, while distal slips from the M. coracobrachialis longus join the distal portion of the same tendon. I would suggest therefore that the tendinous portion of the biceps in *Sphenodon* and the tendon of coracoradialis proprius in *Megalobatrachus* are generically homologous, in so far as they both represent portions of the membranous septum intermuscularis which continues the medial angle of the humerus. These portions respectively have received the insertions of the proximal portion of the biceps (*Sphenodon*) and the muscular part of the coracoradialis proprius (*Megalobatrachus*), and by the mechanical pull of the distal belly of the biceps and its radio-ulnar insertion, in the one case, and the radial insertion of the tendon in the other, have been separated off from the general mass of the intermuscularis connective tissue to become tendinous areas for the respective muscles. The slips in *Megalobatrachus* from the two coracobrachiales show the tendency of these muscles to unite with this tendon in the urodeles, and, as they are similar in situation, derivation and innervation to the two bellies of the

biceps muscle in *Sphenodon*, they may well be regarded as generally homologous to them except for that part of the posterior belly derived from M. brachialis inferior. They are perhaps remnants of a former stegocephalian biceps which has practically disappeared in urodeles to be superseded by the coracoradialis apparatus, conceivably as part and parcel of the general aquatic adaptation which took place in that group. If so, the distal union with M. brachialis inferior has been lost, though its close proximity in *Megalobatrachus* is to be noted, as well as its insertion on both radius and ulna, and the nearness of the radial insertion to that of the tendon of M. coracoradialis proprius. As will be seen, the innervation of M. brachialis inferior is similar to but more distal than that of Mm. coracobrachialis longus and biceps. Therefore all the flexor muscles which enter the upper arm, including the tendons, form a closely related whole in both types, but the muscular part of the coracoradialis proprius is excluded from this relationship, as it possesses the supracoracoid innervation and is, properly speaking, a strictly coracoid muscle which does not enter the upper arm, but merely seizes hold of a tendon that does so.

In *Eryops* (Fig. 48) the tendinous connective tissue region represented as the membrana intermuscularis was doubtless particularly prominent as extending the strong ridge which crosses the humerus diagonally on the posteromedial surface from the pectoral crest to the proximal part of the ectepicondylar expansion. It would thus come into close relation with both coracobrachialis and brachialis inferior, and perhaps could be reached by the most distal part of the supracoracoid mass, thus giving opportunity for the derivation of a biceps through the adherence of radial fibres of the coracobrachialis both distally and proximally, as well as a brachialis inferior union distally, to form an insertion on the lower arm through the intermediary of tendons separated from the connective tissue of the joint. This would give rise to the condition in *Sphenodon*. By the attenuation of the biceps muscle, on the other hand, and by the invasion of the deeper layer of the supracoracoideus, the formation of the coracoradialis proprius of urodeles could be brought about, as the upper limb flexors became less important than chest musculature when terrestrial locomotion with its stresses on the limb flexors gave way to aquatic progression by a swimming movement of the entire limb, more particularly adapted to the evolution of chest and shoulder-girdle musculature.

Brachialis Inferior (Brachialis Anticus)

Figures 19, 44 to 52

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Lateral surface of humerus beneath insertion of Mm. dorsalis scapulæ and procoracohumeralis	<i>Origin</i> From whole lateral and lateroventral surface of the humerus from the processus lateralis humeri to beginning of elbow joint
<i>Insertion</i> Proximal end of radius below insertion of tendon of M. coracoradialis proprius, where it is bounded on either side by Mm. extensor and flexor carpi radialis Also inserts on flexor side of ulna by means of slip from medial side of muscle	<i>Insertion</i> Unites with M. biceps brachii on medial side of elbow joint and inserts in common with it by a double tendon on proximal part of radius and ulna
<i>Innervation</i> N. brachialis inferior from trunk of N. brachialis longus inferior lateralis just distal to the nerve supply of the distal portion of Mm. coracobrachialis longus and biceps brachii	<i>Innervation</i> N. brachialis inferior from lateral branch of N. brachialis longus inferior

That this muscle should be grouped with the system including Mm. coracobrachiales brevis and longus as well as biceps brachii (in reptiles) is shown

- (1) by the related innervation
- (2) by the common insertion with biceps in reptiles, which in turn is largely derived from the coracobrachialis system.

That it is homologous in reptiles and urodeles is shown

- (1) by the homologous innervation
- (2) by the similar origin and insertion
- (3) by the identical position on the ventral side of the forearm
- (4) by the similar location with reference to surrounding muscles, membranes, nerves and blood vessels, provided due allowance is made for the absence of M. biceps brachii in urodeles.

The flexor system of the upper arm in reptiles as exemplified by *Sphenodon* appears to be the generalized arrangement for primitive forms adapted to terrestrial locomotion, while the condition in urodeles as

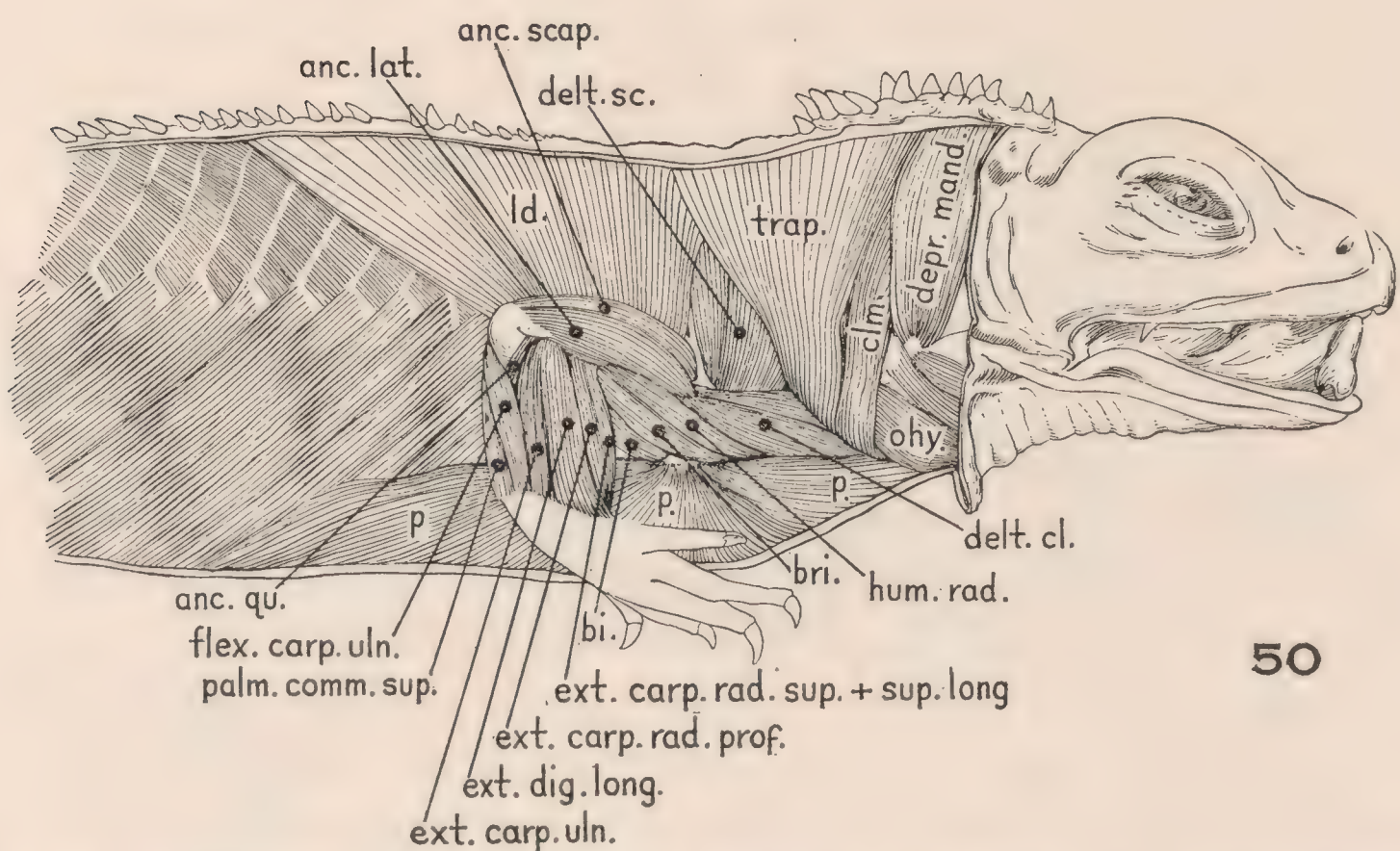
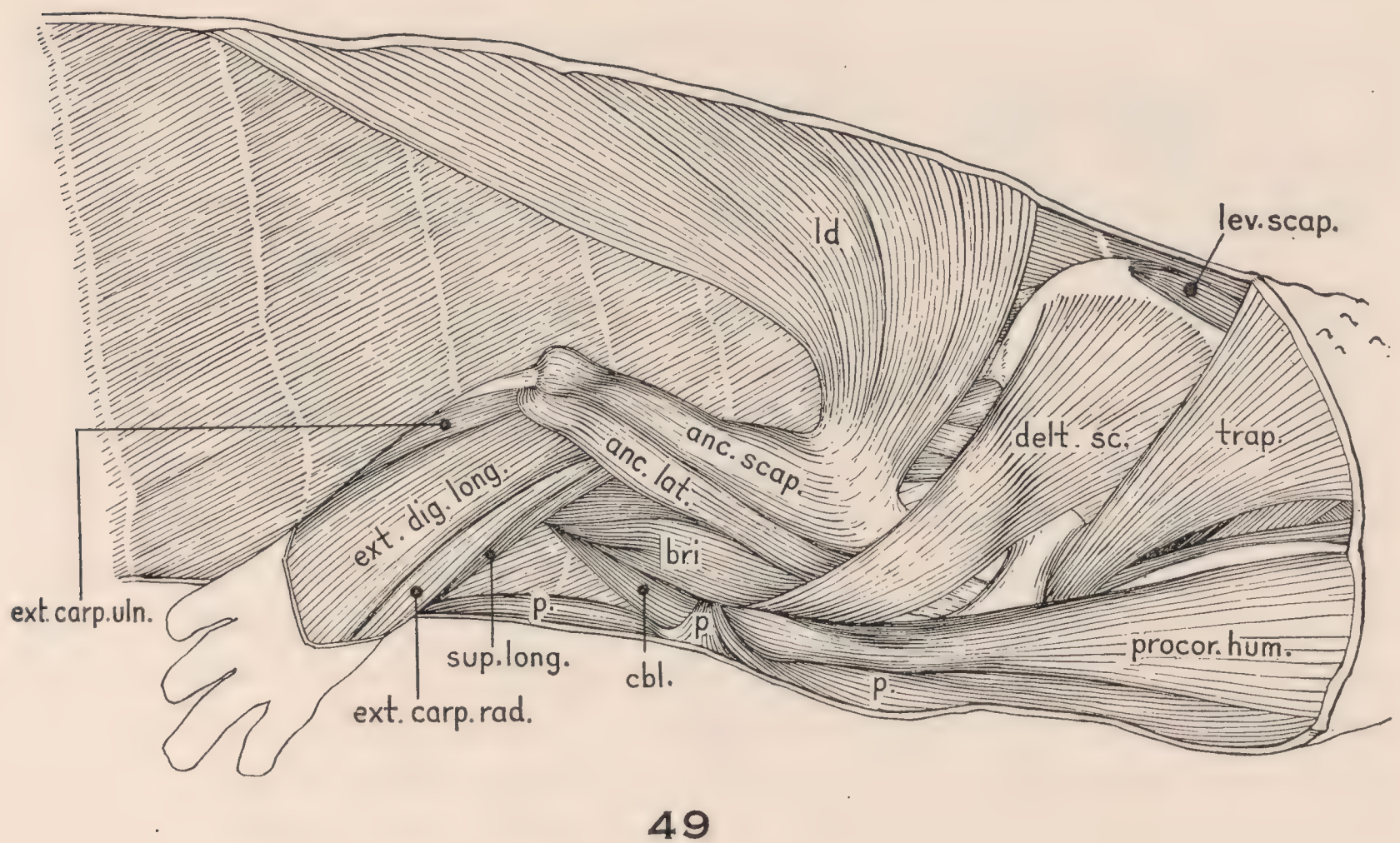


Fig. 49.—Dissection of the superficial shoulder and outer arm musculature of *Megalobatrachus*.

Fig. 50.—Dissection of the superficial shoulder and outer arm musculature of *Sphenodon*.

exemplified by *Megalobatrachus* bears the marks of aquatic adaptation as explained above (page 225). The presence of *M. biceps* is thus interpreted as a terrestrial feature, as compared with its practical disappearance and the substitution of the *M. coracoradialis* in urodeles as aquatic features. Hence we may look for various persisting remains of the typical

condition in the latter group. One of these seems to be the insertion of a slip from the distal end of the M. brachialis inferior on the ulna as well as its proper radial insertion. In *Sphenodon*, the biceps-coracobrachialis complex is the radial flexor of the upper arm, while the brachialis is the ulnar flexor. Both these sets join distally and their insertion by a double tendon on the radius and ulna respectively may possibly be interpreted as an indication of a primitive separate condition in the earliest tetrapod, in which each was the appropriate flexor of the radius and ulna respectively. They also point back to a possible original coalescence of separate radials to form the humerus in a primitive fish ancestor. This is also suggested by the double proximal crests of the humerus and the enlarged duplicate condyles of the distal end, associated with the radius and ulna respectively. Under this conception, the flexor musculature of the upper arm shows a stage of coalescence from a double into a single system, corresponding to that of the anconæus muscle elements on the extensor side. The latter muscle, however, shows a more advanced stage, correlated with its insertion on the dorsally projecting olecranon of the ulna. Both these systems originate partly on the shoulder girdle and partly on the upper arm, but they show a clear convergence from a multiple origin, apparently from separate myotomes, to a more concentrated insertion on the proximal ends of the bones of the lower arm. The flexor series inserts on both lower-arm bones, which can be readily reached by it on this side, and the extensor series inserts only on the ulna, since the position of the radius excludes it from approach by the anconæus series.

The flexor muscles pull in opposition to the anconæus muscles on the principle of a lever of the first order. To offset this pull, when the foot is on the ground and the leg is supporting the body weight, the greater stress must pass through the extensor series over the outer angle of the elbow. Hence the greater consolidation of the anconæus insertion may be correlated with the fact that the ulnar musculature of the lower arm supplies all the fingers of the hand, while the radial musculature is more typically associated with the medial side of the wrist. It may also be correlated with the further fact, as shown by Gregory (1915, pp. 363-4), that the phalanges are the termini of a series of rays which radiate from the distal end of the ulna and bear its weight. The radius and radiale, on the contrary, together with their musculature, are practically excluded from this complex, and, as will be shown later, are dwindling remnants of an ancestral radial system with the prepollex as a terminus (see pp. 266, 290).

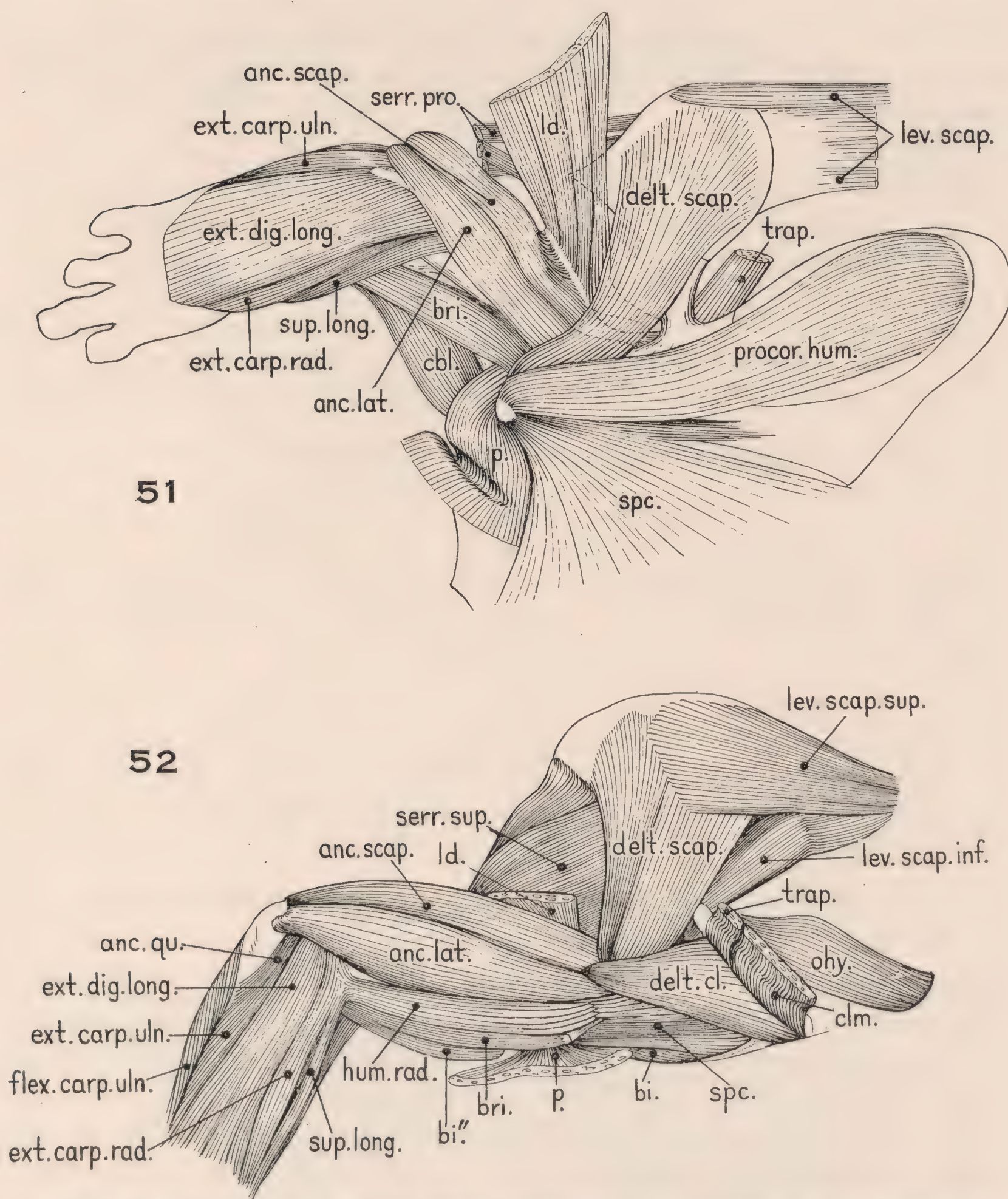


Fig. 51.—Dissection of outer arm and shoulder musculature of *Megalobatrachus*, with certain muscles removed.

Fig. 52.—Dissection of outer arm and shoulder musculature of *Sphenodon*, with certain muscles removed.

The M. brachialis in *Eryops* (Fig. 48) is therefore represented as a muscle inserting on the radius, partly united distally with M. biceps, which in turn is represented as closely associated with the M. coracobrachialis longus as explained above (p. 224), and inserts on the ulna. The distal union of the two muscles is represented as not so complete as in *Sphenodon*.

The location of these muscles is clearly indicated on the bones of *Eryops*, except for *M. biceps*, which from the nature of the case must be inferred.

C. DORSAL MUSCULATURE FROM SHOULDER GIRDLE TO ARM, AND ON UPPER ARM

ProcoracohumeralisDeltoides Clavicularis

(Superficial part)

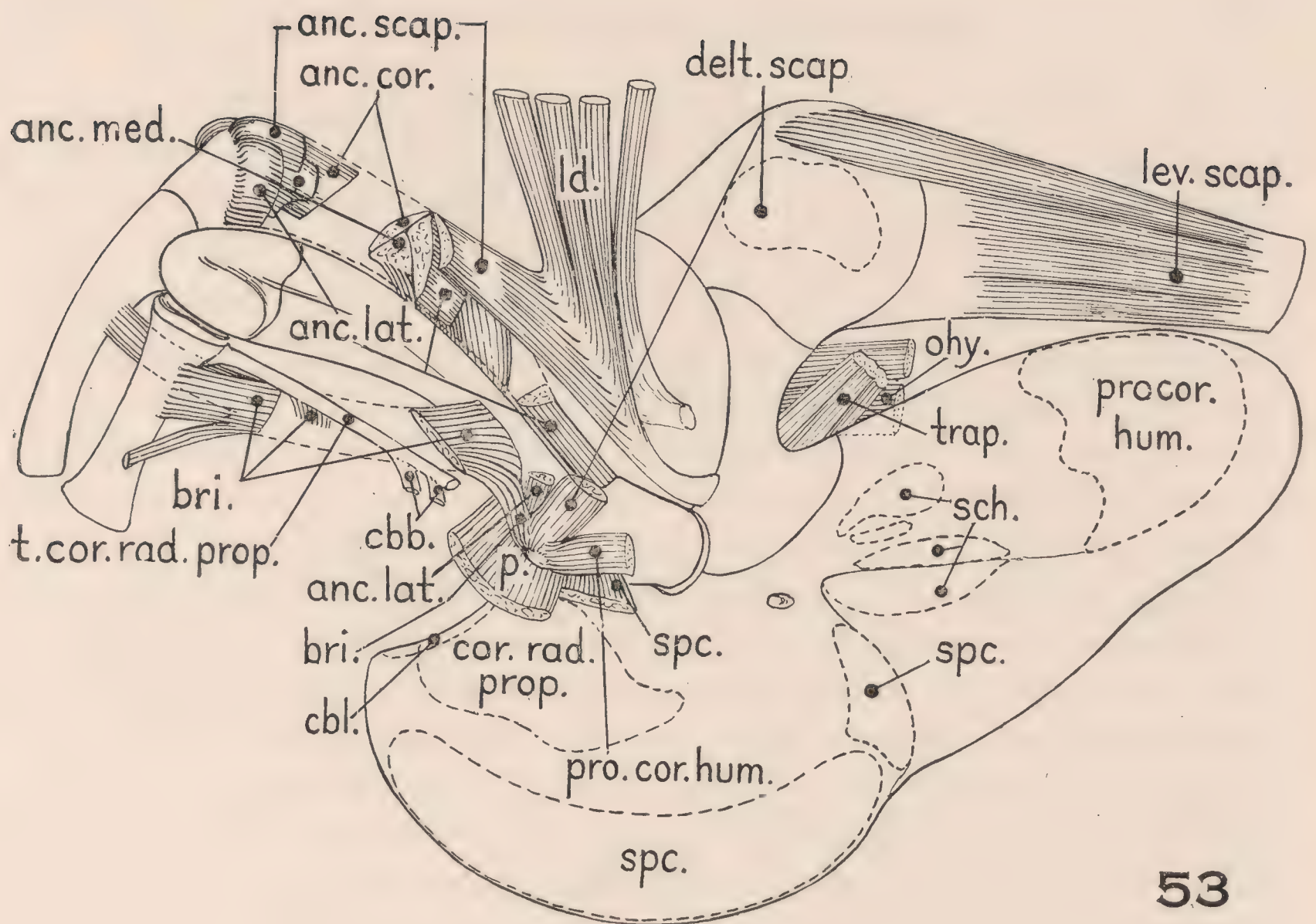
Figures 19, 49 to 57

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Outer surface of anterior end of procoracoid	<i>Origin</i> Outer surface of distal part of clavícula and from episternum
<i>Insertion</i> Processus ventralis humeri above supracoracoideus muscle	<i>Insertion</i> Dorsolateral part of processus lateralis humeri, above supracoracoideus muscle
<i>Innervation</i> N. procoracohumeralis from axillary part of plexus, from same root as N. dorsalis scapulæ	<i>Innervation</i> N. deltoides clavicularis from axillary part of plexus in close association with N. dorsalis scapulæ

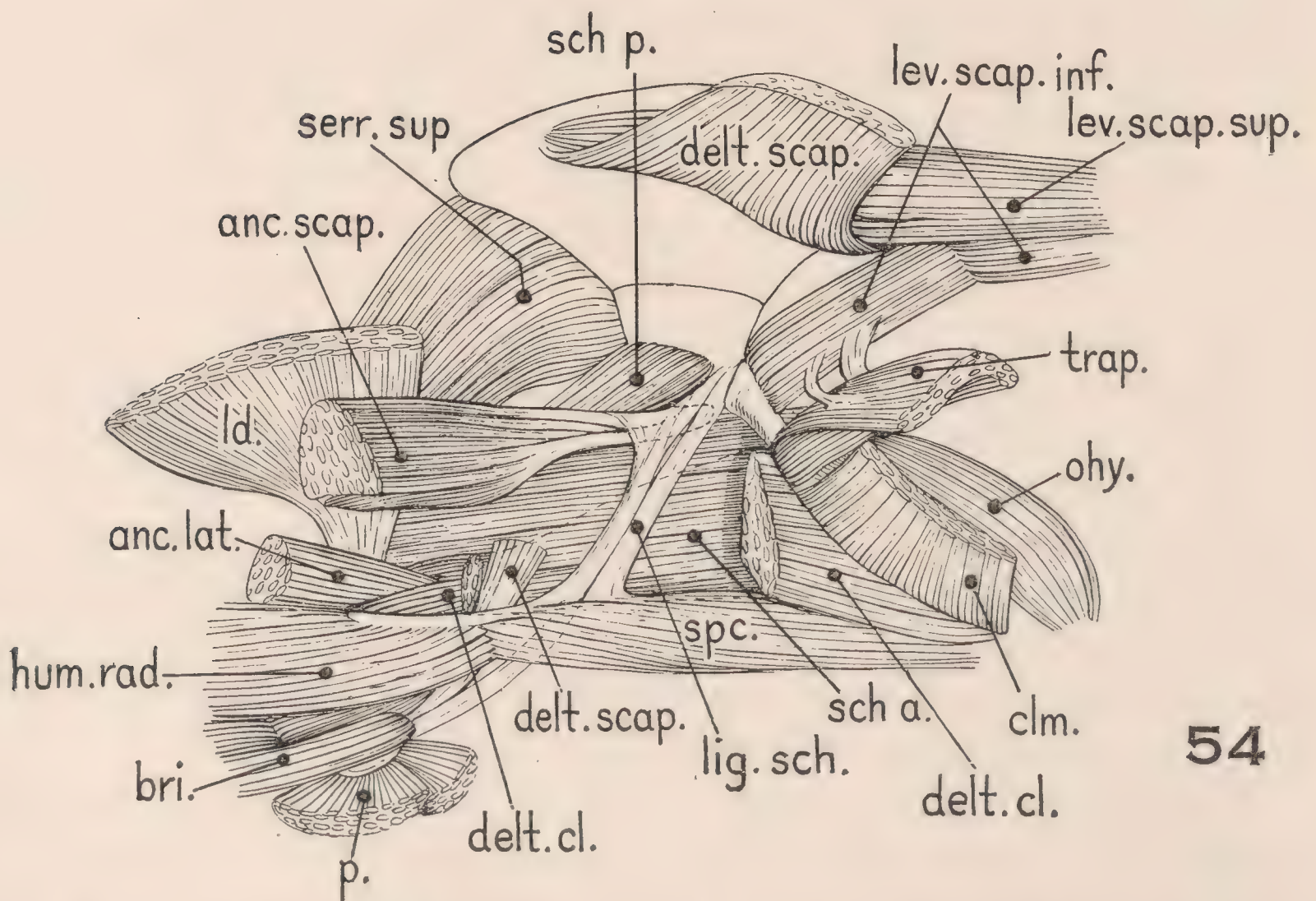
This muscle belongs to the group innervated by the “dorsal” part of the brachial plexus and therefore to the “retractor” or adductor series, speaking in terms of the ancestral fish musculature.¹ As to whether the elements of this group act with the retractor or protractor series in tetrapods depends on the position of their origin and the direction of their fibres with reference to their insertion on the head of the humerus. This varies in different types. In general, however, the muscles of this series pull forward or dorsally, or both, while the muscles of the ventral side, innervated by the ventral nerves of the plexus, pull caudally or ventrally or both.

The most anterior muscles of the dorsal series, e.g., the deltoides clavicularis, the scapulohumeralis anterior and the humeroradialis externus, are contiguous to the supracoracoideus and the pectoralis episternalis, which are the most anterior muscles of the ventral series,

¹Since this paper was sent to press, a very interesting article by A. S. Romer has appeared (1924), in which he divides the main muscle masses of the tetrapod limb into a dorsomedial and ventrolateral group, as derived from the adductor and abductor muscle masses of the fish fin respectively. He includes the deltoid (axillary) series with the latter, thus differing from my interpretation. This view demands careful consideration, and will be dealt with in a supplementary paper.



53



54

Fig. 53.—Dissection of deeper muscles of the upper arm and shoulder girdle of *Megalobatrachus*, showing origins and insertions.

Fig. 54.—Dissection of the deeper muscles of the shoulder region of *Sphenodon*, with especial reference to the ligamentum scapulo-humerale laterale (lig. sch.)

though the former, with its separate and anterior innervation, scarcely included in the brachial plexus, really occupies a somewhat anomalous position, neither dorsal nor ventral. The scapulohumeralis anterior and supracoracoideus muscles, as Romer has pointed out (1922, p. 533), blend into each other, and because of this he is led to group them together. I cannot agree with this because of the separate innervation, which Romer mentions but fails to emphasize in its true significance. It is certain that innervation, wherever recognizable, is a criterion which must throw light on the history of the muscle or part of the muscle concerned, as has been pointed out by many authors (Fürbringer, Johnston, Kingsley, etc.) hitherto. It is also certain that mere contiguity, or even blending of muscles and the consequent "double innervation," cannot be taken seriously as an indication of a common origin. Double or multiple innervations indicate derivation from separate muscle units which have become blended into an apparently "single" muscle mass. This same argument applies to Romer's contention (*loc. cit.*) that "separation (of the supracoracoid) from the coracobrachialis is an entirely artificial one." These are clearly muscles of very diverse relationship, as shown above, though they happen to be situated so as to practically blend into each other on their contiguous borders. This matter will be further dealt with in connection with the discussion of the Mm. scapulohumerales.

I agree with both Watson (1917a, p. 4) and Romer (1922, p. 529) in connecting the history of the two deltoid muscles with the fate of the dermal girdle. In *Sphenodon* (Fig. 56), the M. deltoides clavicularis arises from the dermal clavicle. This is true in all forms in which the clavicle remains. In *Megalobatrachus* (Fig. 55) the clavicle has disappeared along with the rest of the dermal limb skeleton, depositing the origin of the deltoides clavicularis muscle bodily on the underlying and greatly elongated procoracoid, thus transforming the muscle into a procoracohumeralis. The insertion of course remains the same, being located on the deltoid crest posterodorsal to that of deltoides scapularis (dorsalis scapulæ), and above that of M. suprascapularis. Both muscles are innervated similarly by a nerve that arises in close association with the N. dorsalis scapulæ. The homologies are therefore clear.

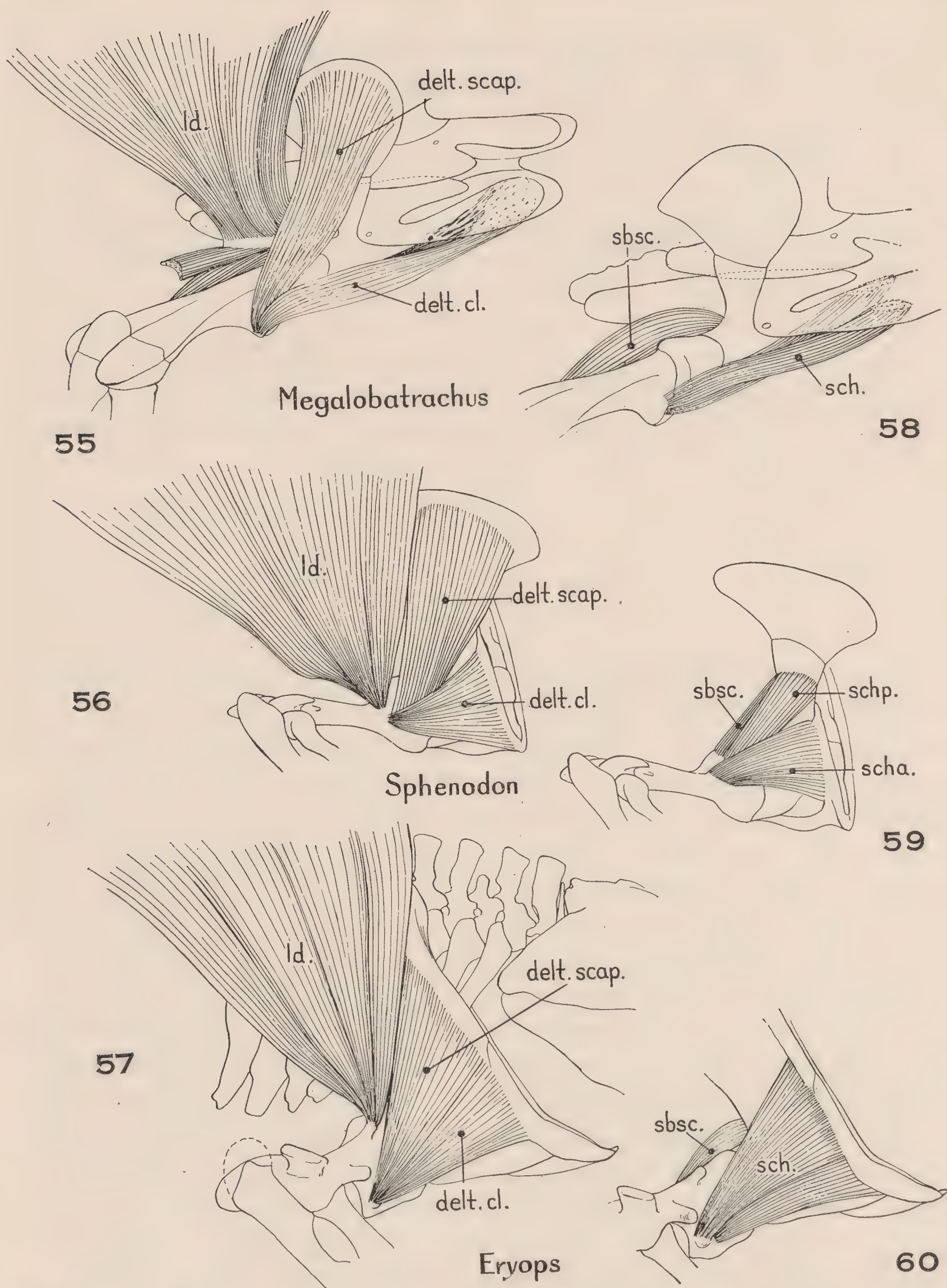
As *Eryops* (Fig. 57) possessed a well-developed dermal clavicle, and a conspicuous deltoid crest on the humerus head, the restoration of a deltoides clavicularis is a simple matter. Its relation to the M. dorsalis scapulæ is discussed below.

Dorsalis Scapulæ (Deltoides Scapularis)

Figures 19, 49 to 57

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Kidney-shaped area occupying center of cartilaginous suprascapula, leaving borders free	<i>Origin</i> Anterior three-fourths of ventral part of suprascapula and dorsal corner of bony scapula
<i>Insertion</i> Lateral surface of processus ventralis humeri, anterodorsal to M. procoracohumeralis and close to M. supracoracoideus	<i>Insertion</i> Dorsally on processus lateralis humeri, anterodorsal to M. deltoides clavicularis and dorsal to M. supracoracoideus
<i>Innervation</i> N. dorsalis scapulæ from axillary stem	<i>Innervation</i> Nn. dorsales scapulæ from axillary stem and from N. supraclavicularis

As shown above, the origin, insertion and innervation of this muscle are similar in *Sphenodon* and *Megalobatrachus*. They may therefore be considered homologous. This is also confirmed by the similar relations to the neighboring muscles. There are, however, certain differences correlated with the divergent evolution of the skeleton in the two groups to which the types belong. Thus in *Sphenodon* (Fig. 56), the M. dorsalis scapulæ is closely associated along its anteroventral border with the dorsal border of M. deltoides clavicularis, while in *Megalobatrachus* (Fig. 55) the muscles are widely separated except at their insertion, by the wide divergence of the procoracoid from the scapula and its prolongation forward. It is evident from the innervation of the two muscles and their contiguous insertion, that they are genetically related, while their superficial position and the association of the deltoides clavicularis with the dermal girdle suggest that both were originally associated with dermal portions of the skeleton. In *Eryops* and all known stegocephs, as well as in the primitive reptiles, the cleithrum is the dermal element associated with the scapula in the same way that the clavicle is associated with the procoracoid. In *Eryops*, the dorsalis scapulæ would inevitably find its origin on the cleithrum and the portion of the scapular blade immediately posterior to it, just as the deltoides clavicularis would arise from the clavicle and the procoracoidal region adjacent. The clavicle and cleithrum, however, form with the interclavicle a continuous collar of bone on the anterior border of the girdle, thus suggesting the continuity



Figs. 55, 56, 57.—Comparison of the latissimus dorsi and deltoid muscle system of *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*.

Figs. 58, 59, 60.—Comparison of the scapulohumerales and subscapularis of *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*.

of the origins of the two muscles. This and their community of innervation in later forms justify the inference of their origin from a single muscle mass in Stegocephalia, and they are so indicated in their restoration in *Eryops* (Fig. 57).

It seems evident that their divergence into two muscles in later forms is correlated with the dwindling of the cleithrum, as pointed out by Romer (1922, p. 529), the origin of the dorsal portion following the degenerating cleithrum up into the suprascapula (which is a cartilaginous expanse functionally replacing the dermal cleithrum in all later vertebrates, as the procoracoid replaced the clavicle in urodeles), while the ventral portion of the muscle mass was retained in its ancestral relation to the clavicle, the acromion being left to mark the original point at which the two portions were originally joined in the stegoceph ancestor, i.e., the junction of the primordial cleithrum and clavicle.

Schmalhausen (1917) has shown that in various genera of Anura (*Pelobates*, *Hyla*, *Pipa*, *Xenopus*, *Bombinator* and *Alytes*) a dermal ossification appears in the anterior border of the suprascapula, in the position of the stegocephalian cleithrum, with which he finds good reason to homologize it. This later becomes the suprascapular bone and is associated with the *deltoides clavicularis*. It seems clear that in the Amphibia the original single deltoid muscle divided as the cleithrum dwindled, and that this dwindling took place upward, separating the two dermal elements and carrying the *dorsalis scapulæ* part of the deltoid muscle with it.

The fact that so many important muscles find their origin or insertion in *Sphenodon*, on both the outer and the inner side of the cleithral region of the suprascapula, i.e., on the anterior and dorsal surface, strengthens the view that the cleithrum formerly occupied this region as a strengthening element. As it disappeared in both reptiles and urodeles, a wide cartilaginous expansion took its place to replace a strong and localized area of origin, stressed by a short and somewhat perpendicular pull in short-limbed forms like *Eryops*, with a wide cartilaginous area from which the proportionately longer muscles of later types pulled in a more parallel direction.

In small forms like *Sphenodon* and the smaller lizards, this cartilaginous expansion distributes the pull over a large surface, counteracted by the similar pull of muscles on the opposite face of the suprascapula, and further supported by the closeness with which the suprascapula is bound to the side of the body by the more superficial musculature, acting like a series of bandages over its outer surface. In larger reptiles like the croco-

dile, this is not sufficient, and here we find a proportionately small suprascapula well ossified, and a much larger and longer bony scapula resembling that of *Eryops*, in which the mechanical conditions were similar. The urodeles went much further in the cartilagizing of the skeleton. Here most of the group are aquatic forms and the stress on the skeleton is still less, while the cartilaginous expansions of suprascapula, coracoid and procoracoid are much greater, with the muscle origins on these elements proportionately expanded. In the more terrestrial anurans, however, we again find a dwindling of cartilage and a strengthening of the bony girdle in proportion, with a corresponding narrowing of the muscle origins. Here also the dermal skeletal elements are more largely retained.

These adaptive features must be taken into consideration in any attempt to homologize the muscles and skeleton of the respective types.

Scapulohumeralis Anterior
Figures 19, 53, 54, 58, 59, 60

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Represented by two slips arising on the procoracoid beneath and resembling deeper slips of the M. procoracohumeralis	<i>Origin</i> Ventral part of outer surface of the bony scapula and dorsal anterior part of coracoid, ventral to tendinous origin of M. anconæus scapularis and origin of M. scapulohumeralis posterior
<i>Insertion</i> Outer surface of humerus immediately anterior to insertions of Mm. procoracohumeralis and dorsalis scapulæ	<i>Insertion</i> Extensor surface of humerus head immediately dorsal to insertion of Mm. latissimus dorsi, dorsalis scapulæ and deltoides clavicularis
<i>Innervation</i> Axillary innervation	<i>Innervation</i> N. scapulohumeralis from the axillary bundle

This muscle is evidently a deeper portion of the deltoid muscle system as shown by the following points.

(1) In *Sphenodon* (Figs. 54, 59), it lies directly beneath the deltoides clavicularis, with its origin beneath and directly posterior to that of the latter muscle, and its fibres follow the same course.

(2) The insertion is on the head of the humerus on an area contiguous to that of the deltoid, which being superficial inserts on the high deltoid crest while the scapulohumeralis inserts dorsally but beneath it.

(3) The innervation is axillary in intimate association with that of the Mm. deltoides clavicularis and dorsalis scapulæ.

It is not related to the supracoracoideus, as described by Romer (1922, p. 533), if we follow the criterion of innervation which is here widely separated in its origin from that of the supracoracoideus. The blending of the muscles on their contiguous margins gives an impression of a single muscle system with a "double" innervation, but this is not a tenable conception, if muscles are to be genetically associated with the nerves that supply them. In urodeles, as Romer states, the procoracohumeralis appears to have a double innervation, but it is evident from the conditions in *Megalobatrachus*, as shown below, that there is an invasion of the procoracoid region by supracoracoideus fibres and a tendency to weld with some of the deeper fibres of the procoracohumeralis. In this connection, see the preceding discussion of the supracoracoid muscle.

This muscle hitherto has been considered absent from urodeles. My dissections of *Megalobatrachus* (Figs. 39, 41), however, show two irregular slips arising from the outer surface of the procoracoid beneath the procoracohumeralis and proximal to its origin, which insert dorsal to and beneath the deltoid crest and the insertion of the procoracohumeralis and occupy the same position that the scapulohumeralis anterior occupies in *Sphenodon* (Figs. 54, 59) with reference to the deltoides clavicularis, which as we have seen must be regarded as homologous to procoracohumeralis.

These slips are also innervated by branches of the axillary nerve, and hence are apparently homologous to M. scapulohumeralis anterior of *Sphenodon*.

Again there is a tendency in *Megalobatrachus* for a migration of the supracoracoideus elements toward the procoracoid, for an inner slip in my dissection has apparently separated from the lateral edge of the supracoracoid mass and invaded the membranous area, bridging the gap between the coracoid and the procoracoid. This slip possesses a supracoracoid innervation.

Anthony and Vallois (1914, pp. 251-271) have shown in Anura that portions of the procoracohumeralis and supracoracoid have fused, carrying their respective innervations with them, and forming a so-called acromiohumeralis with a double innervation. They regard these fused halves, however, as derived from the supracoracoid and axillary systems respectively.

As above mentioned, we have here an instance of the close approach of the dorsally innervated and ventrally innervated muscle systems of the arm in the anterior part of the limb anlage where the two rotate anteriorly about the shoulder girdle until they meet and fuse their fibres.

In *Eryops* (Fig. 60), as an ancestral and primitive form, I regard this muscle as a deeper portion of the deltoideus, arising on the scapulo-coracoid just posterior to the origin of the deltoid, and inserting on the head of the humerus in the position indicated in both *Sphenodon* and *Megalobatrachus*.

Scapulohumeralis Posterior
Figures 19, 53, 54, 58, 59, 60

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Same as M. scapulohumeralis anterior	<i>Origin</i> From bony scapula dorsal to origin of Mm. anconæus scapularis and scapulohumeralis anterior
<i>Insertion</i> Same as M. scapulohumeralis anterior	<i>Insertion</i> Extensor surface of humerus head on distal end of tuberculum mediale dorsal to insertion of M. scapulohumeralis anterior
<i>Innervation</i> Axillary innervation	<i>Innervation</i> N. scapulohumeralis from the axillary bundle

There is no muscle slip to correspond to this in urodeles. Its characteristic feature appears to be that it arises from the scapula on the area posterior to the acromion and inserts on the head of the humerus just dorsal to the insertion of the scapulohumeralis anterior, separating it from the insertion of the M. subcoracoscapularis.

Romer (1922, pp. 530–533) regards it as an offshoot of the latter and unrelated to the M. scapulohumeralis anterior, basing his view on the fact that the tendinous origin of the M. anconæus scapularis arises between the two muscles and “sets them off clearly” from each other. I am unable to agree with this view, firstly, because the two Mm. scapulohumerales are innervated by branches of the same nerve, which arises from the axillary stem in much closer relationship to the deltoid innervation than to that of the M. subcoracoscapularis, and, secondly,

because Fürbringer (1900, Pl. xv) in an admirable series of comparative figures has shown (though in another connection) that in various reptilian types the place of origin of the tendon of *M. anconæus scapularis* is extremely variable in various genera. I am strongly inclined to the view that it is a greater forcing of the issue in homologizing muscles to disregard such a fundamental matter as related innervation in favor of variable tendinous origin than to take the opposite ground.

Again, the occurrence of a separate scapulohumeralis posterior is rare in reptiles. While, as Fürbringer has shown (1900, p. 489), both muscles are preserved in *Sphenodon*, only scapulohumeralis anterior occurs in the majority of lizards, and only the posterior muscle in the crocodile. Both muscles also occur in birds. This seems to indicate considerable variability in the area of an original scapulohumeralis mass, which, like the deltoid, was doubtless originally single, but early divided into two slips as seen in *Sphenodon*, and as inherited by birds from their primitive diapsid stock, while, as Fürbringer states, the anterior muscle degenerated in crocodiles and the posterior muscle in the majority of modern lizards. It is easy to comprehend how this variableness in both the scapulohumeralis muscle and the place of origin of the tendon of *anconæus scapularis* would make it possible first for the latter to shift to its position as in *Sphenodon*, and then for a posterior slip to split off from the scapulohumeralis mass and grow dorsally to the tendon. The shifting powers of the *M. scapulohumeralis* are well shown in Fürbringer's figures. The innervation therefore remains the most constant criterion and definitely relates the two slips of this muscle to each other.

In *Eryops* (Fig. 60), the *M. scapulohumeralis* is inferred as a single mass arising from the outer surface of the scapulocoracoid as a deeper layer of the deltoid and inserting on the head of the humerus between the *processus lateralis* and *medialis*.

Latissimus Dorsi

Figures 19, 22, 23, 49 to 57, 61

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Dorsal fascia opposite vertebræ by four slips	<i>Origin</i> Dorsal aponeurosis extending from vertebræ 6-17
<i>Insertion</i> Most anterior slip on a tendinous arch extending from posterior border of bony scapula to the tendinous investiture of the joint capsule Three posterior slips on upper side of tendinous portion of anconæus scapularis which terminates as the tendon of origin of that muscle	<i>Insertion</i> Proximal outer surface of humerus head ventral to insertion of M. scapulo-humeralis anterior and antero-dorsal to anterior part of origin of M. anconæus lateralis and postero-dorsal to the insertion of M. deltoides clavicularis
<i>Innervation</i> N. latissimus dorsi from N. brachialis longus superior in association with base of axillary bundle	<i>Innervation</i> Nn. latissimi dorsi from N. brachialis longus superior in association with origin of axillary bundle

This muscle is clearly identified in all reptiles and urodeles. It arises in varying extent from the dorsal fascia of the back, spreading over several segments. Through the influence of the segmented connective tissue over which its origin has spread, it gives a superficial impression of being a segmental muscle. That it belongs properly, however, to the arm is shown, firstly, by its ontogenetic origin from the blastema of the arm muscles; secondly, by its insertion on the humerus or fascia of the humerus musculature, and not on the girdle as in the case of the true segmental muscles; thirdly, by its innervation, which arises in close association with the origin of the axillary nerve trunk from the plexus, thus relating it in general to the deltoid group of muscles; fourthly, the insertion in *Sphenodon* is on the head of the humerus at its junction with the shaft between the origins of Mm. anconæus lateralis and medialis, and in close association with the insertions of Mm. deltoides clavicularis and scapulohumeralis posterior. This association of axillary insertions with the insertion of M. latissimus dorsi is a further confirmation of its affinities with the deltoid group. It will be noted that this muscle corresponds to the pectoral muscle on the ventral side and opposes it in the elevation and depression of the limb as a whole.

In *Megalobatrachus*, there is a similar origin. The insertion, however, does not reach the humerus, but the posterior three-fourths of the muscle inserts on the upper side of a tendinous band which runs forward obliquely to the posterior angle of the scapula to become the tendon of origin for the *M. anconæus scapularis*. This muscle unites with the under side of the tendinous band directly opposite the insertion of *M. latissimus dorsi*. The anterior one-fourth of the *latissimus* inserts on a tendinous arch which extends from the fascia of the joint capsule to the posterior border of the scapula, and it is continuous with the connective tissue in which the brachial plexus is imbedded. This difference as compared with *Sphenodon* is doubtless due to the comparatively incomplete ossification of the humerus in urodeles. The bone barely reaches the head of the humerus, which is entirely cartilaginous, and is contained in a capacious membranous capsule imbedded in much connective tissue. The *anconæus scapularis* and the *latissimus* have apparently formed their common tendon by inserting their fibres in this connective tissue, from which an outer strip continuous with the scapula separated through their common pull. In *Sphenodon*, as well, there is much connective tissue in this region, and the insertion of the *latissimus* is on a part of the humerus head that is cartilaginous in *Megalobatrachus*. The condition in the latter form is, without doubt, a simplification due indirectly to aquatic adaptation.

In *Eryops* (Figs. 18, 19, 57), the completely ossified humerus head exhibits a bony protuberance on its anterodorsal border which corresponds in position with the rugosity on which the muscle inserts in *Sphenodon*, and which is clearly intended for the *latissimus dorsi*. The antero-posterior expansion of the muscle origin can be inferred only from the position of the scapula which doubtless marked its anterior border, and from the weight of the body which must have necessitated a considerable posterior development.

Subcoracoscapularis

Figures 19, 58 to 61

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> From the posterior margin of the lower third of the bony scapula, and the adjacent margin of the coracoid as far as the origin of <i>M. anconæus coracoideus</i>	<i>Origin</i> By two heads (a) Very well developed. From whole dorsal surface of the coracoid except the medial and caudal borders (b) Caudal rim of bony scapula, somewhat ventral from insertion of <i>M. serratus superficialis</i>
<i>Insertion</i> Proximal half of the medial angle of the humerus	<i>Insertion</i> Both parts unite and converge strongly as they pass over the shoulder joint and insert on the processus medialis by means of a powerful tendon
<i>Innervation</i> N. subcoracoscapularis from N. radialis superior	<i>Innervation</i> N. subcoracoscapularis arising near root of N. axillaris from N. radialis superior

This muscle is very powerful in *Sphenodon*, rising from a greater part of the inner surface of the coracoid, as well as from the posterior edge of the scapula. It converges to the processus medialis to insert in a small area by a strong tendon.

In *Megalobatrachus* (Fig. 61), its area of origin is much more contracted, being localized on the posterior edge of the scapula and coracoid through about one-third the extent of each. It is nevertheless a strong muscle, the extent of its insertion compensating for the comparatively reduced origin as compared with *Sphenodon*, for it attaches along fully one-half the length of the humerus.

The innervation indicates that it should be grouped with the axillary muscles that insert on the humerus head. Osawa (1898, p. 558) assigns it a second innervation from the N. coracobrachialis, but this is denied by Fürbringer (1900, p. 440), and I can see no evidence of it in my dissections. He also gives a double innervation to the muscle in *Megalobatrachus* (*Cryptobranchus*), from Nn. radialis superior and pectoralis, but I cannot confirm the latter. Such an innervation would be surprising in either case, and unless definite evidence to the contrary should materialize, these muscles should be regarded as related to the axillary system.

As Romer has pointed out (1922, pp. 530–531), it is difficult to believe that in the primitive reptile this muscle had an extensive coracoid origin. In *Eryops*, this part of the muscle probably arose from the posterior edge of the supraglenoid buttress, and the scapular portion from the normal region on the posteromedial surface of the scapular blade, where the modeling of this surface presents a convenient area of attachment. The processus medialis is directed toward both of these areas.

We thus have a series of fan-shaped muscles related to the deltoid group inserting around the head of the humerus and arising from the girdle, the superficial fascia of the back and the superficial fascia or

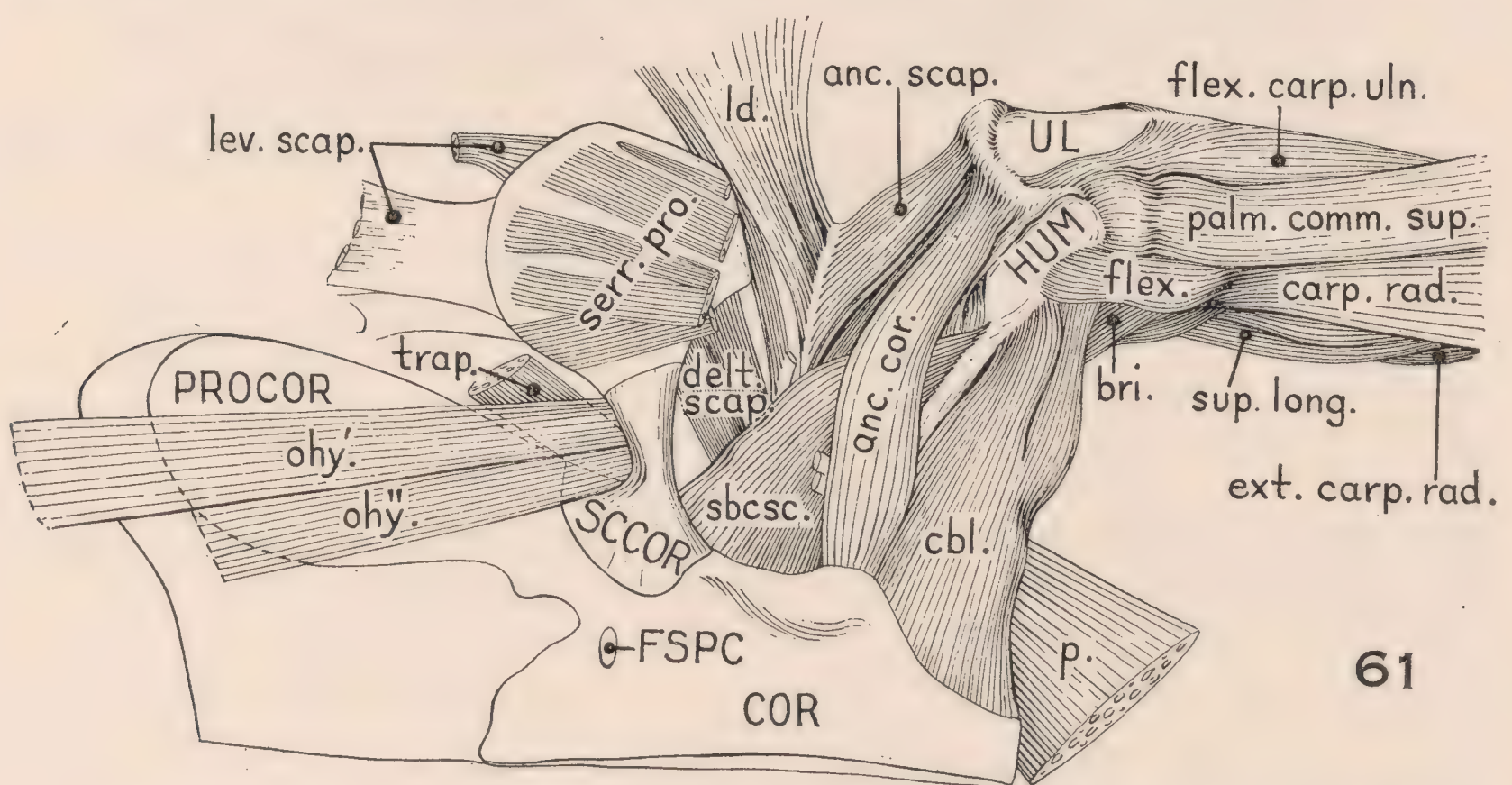


Fig. 61.—Dissection of the inner upper arm and shoulder musculature of *Megalobatrachus*.

dermal skeleton of the chest. The dorsally located muscles are all innervated from the axillary nerve or from nerves arising in association with it, while the ventrally situated pectoral muscle with its widely divergent subdivisions is innervated by the pectoral nerve, which branches from the ventral side of the plexus in association with the root of the N. brachialis longus inferior, in a similar and somewhat symmetrical manner to that by which the axillary nerve and its associates arise from the dorsal side of the plexus in association with the root of the N. brachialis longus superior.

The supracoracoideus muscle, on the other hand, is the most anteriorly placed of the series of muscles that pass from the girdle to the head of the humerus. It is placed like a keystone between the dorsal and ventral

musculature, and is correspondingly innervated by the most anteriorly situated nerve of the plexus, the supracoracoid nerve, which can hardly be reckoned as belonging to either the dorsal or ventral side of the plexus, with which it barely connects and then shunts off. It occupies a similar relation in all tetrapods. Thus, muscles arising on the girdle or on the body fascia and inserting on the outer side of the humerus head may be divided into three classes, as follows:

1.—THE DORSAL MUSCLES (axillary and associated innervation)

- (a) *Latissimus dorsi*
- (b) *Dorsalis scapulæ*
- (c) *Deltoides clavicularis*
- (d) *Scapulohumerales* anterior and posterior
- (e) *Subcoracoscapularis*

2.—THE ANTEROMEDIAN MUSCLES (supracoracoid innervation)

- (a) *Supracoracoideus*
- (b) *Coracoradialis proprius* (inserts on a tendon in the neighborhood of the humerus head)

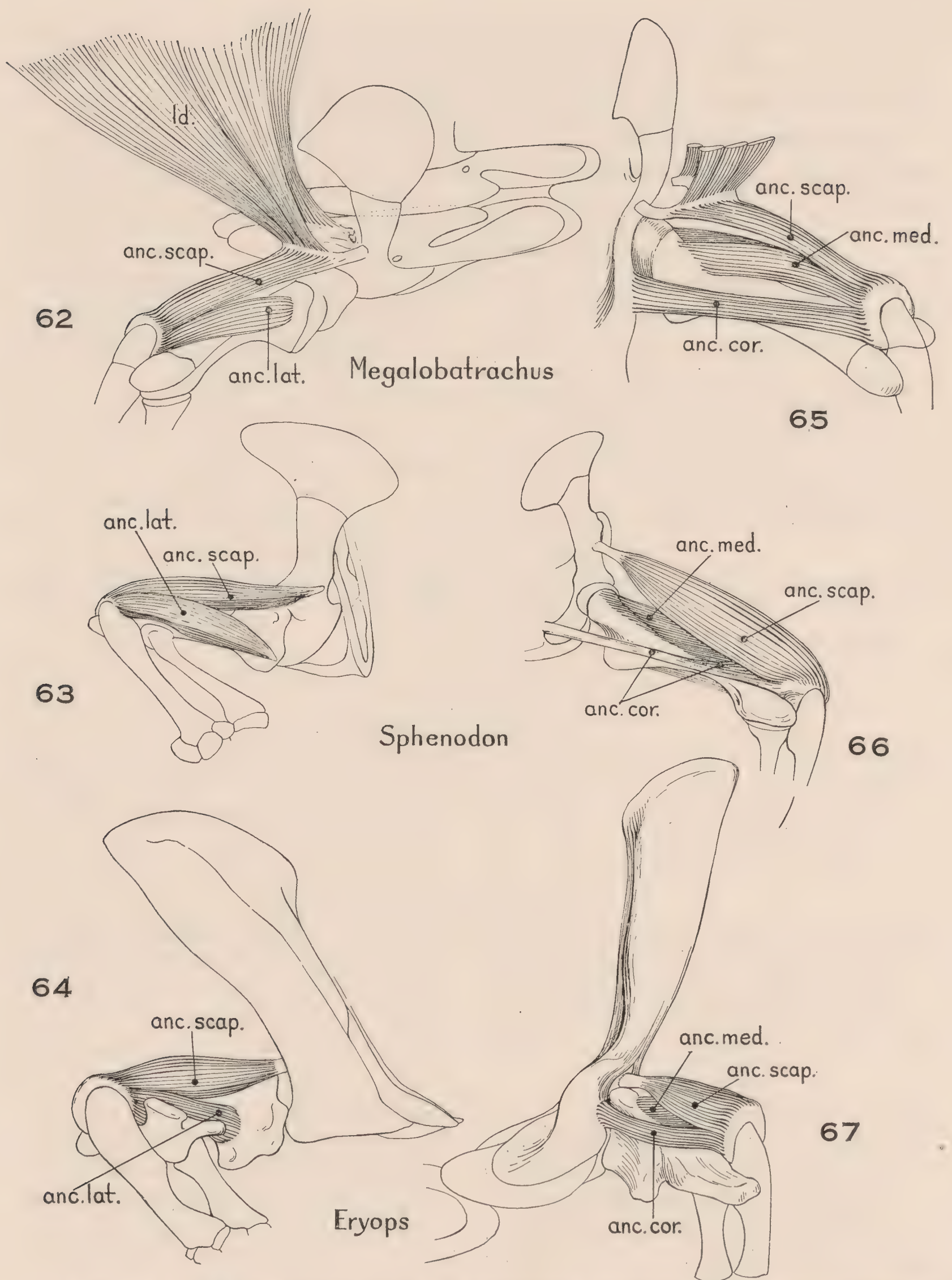
3.—THE VENTRAL MUSCLES (pectoral innervation)

- (a) *Pectoralis*

Anconæus (Triceps)

Figures 19, 22, 23, 49 to 54, 61 to 67

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> (1) <i>Scapulo</i> (a) Anconæus By means of a tendon arising from the posterior border of the scapula close to the glenoid and also from the joint capsule passing upward between the M. latissimus dorsi and the muscular part of A. scapularis to form the insertion of the former and the origin of the latter	<i>Origin</i> humeral part us scapularis By means of a tendon arising from the lateral surface of the scapula between the origins of Mm. scapulohumerales anterior and posterior
(b) Anconæus Proximal one-fourth of anterolateral surface of humerus shaft along its superior angle	humeralis lateralis Entire anterolateral surface of the humerus shaft
(2) <i>Coraco</i> (a) Anconæus Narrow muscular origin from posterior angle of coracoid between origin of M. subcoracoscapularis and M. coracobrachialis longus	humeral part us coracoideus Tendinous band arising from posterior angle of coracoid between origin of M. subcoracoscapularis and M. coracobrachialis longus
(b) Anconæus Dorsomedial surface of humerus including distal part of processus medialis and extending along proximal half of shaft	humeralis medialis Dorsomedial surface of humerus including distal part of processus medialis and extending along proximal half of shaft
<i>Insertion</i> (1) (a) unites with (1) (b) (2) (a) unites with (2) (b) and the joined slips unite to insert as one muscle around the tendinous capsule of the olecranon of the ulna	<i>Insertion</i> (1) (a) unites with (1) (b) (2) (a) unites with (2) (b) and (1) (b) then all converge as one muscle to unite around the proximal end of the ulna in a semicircular insertion
<i>Innervation</i> Nn. anconæi from Nn. radiales inferior and superior	<i>Innervation</i> Nn. anconæi from N. brachialis longus superior



Figs. 62, 63, 64.—Comparison of the anconæus musculature of *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*, as seen from the outer side of the arm.

Figs. 65, 66, 67.—Same as seen from the inner side of the arm.

There is no doubt as to the general homology between the anconæus of reptiles and that of urodeles. As shown in both *Sphenodon* and *Megalobatrachus*, it is the general extensor muscle of the upper arm. It corresponds to, and acts in opposition to the coracobrachialis, biceps-brachialis mass of the ventral surface of the humerus. The homologies of the slips which compose it, however, have certain difficulties. It may be well, therefore, to consider them successively.

The four slips composing the anconæus may be divided vertically, as shown in the table, into two main groups, each composed of a head originating on the girdle and a head arising from the humerus; or they may be grouped horizontally into a superficial set composed of the two zonal heads, anconæus scapularis and anconæus coracoideus, and a deeper set composed of the two humeral heads, anconæus humeralis lateralis and anconæus humeralis medialis. Originally, they may have formed one mass, which occupied the two dorsal faces of the humerus, shown very effectively, as Romer has pointed out (1922, pp. 555–556), by *Acheloma* and by *Eryops*, to consist of the two upper faces of the primitive tetrahedral humerus, with its mutually alternating triangular surfaces. It is likely that the ridge connecting the humerus head with the supinator crest, which is very prominent in these two types and sets the two surfaces off at right angles with each other, is correlated with the division of the deeper anconæus layer into two slips diverging proximally. Along this ridge the insertion of the latissimus dorsi thrusts itself still further, separating these two anconæus heads. In later reptiles, the latissimus dorsi inserts between the origins of the muscle slips in question. The two superficial slips, anconæus scapularis and anconæus coracoideus, are likewise separated by this muscle, hence it becomes natural to group them with the respective deeper portions. As a rule, each deeper slip tends to unite with the superficial slip above it before all join to insert on the ulna. Hence the classification shown in the table becomes a natural one. In later Amphibia, the latissimus dorsi either does not reach the humerus or inserts so far proximally as not to divide the anconæal mass.

(a) *Anconæus Scapularis* (Figs. 62 to 67). Primitively, this slip originated from the dorsal part of the fibrous connective tissue enwrapping the joint capsule, as is still the case in *Necturus* (Wilder, 1912, p. 393). This portion separated to form a tendon closely associated with the capsule, and clinging to it at its junction with the base of the scapula, as in *Megalobatrachus* (Figs. 53, 62, 65), and in *Salamandra* (Perrin, 1899, p. 255). This is the general condition in urodeles and anurans. In reptiles there is considerable specialization. For example, in *Sphenodon*

(Fig. 54), where the most extreme condition is reached, the anconæus scapularis arises from the outer surface of the bony scapula at about the middle point, between the origins of the two Mm. scapulohumerales. On this account Romer regards this as the morphological posterior border of the scapula (1922, p. 531). However, because of the notorious variability both of this tendon and of the origin of M. scapulohumeralis (p. 239), especially as shown by Fürbringer's excellent figures (1900, Pl. xv, Fig. 142), I believe that the position of the tendon in *Sphenodon* is secondary, having been shifted anteriorly in correlation with the strong development of the scapulohumeralis muscles which are both present in this form, arising in an anterior position on the girdle. In changing its position it carried with it a portion of the connective tissue of the capsule as a vertical slip to form the ligamentum scapulohumerale laterale. Fürbringer's figures (1900, Pl. xv) show all degrees of transition in various genera of lizards between this extreme condition and that in *Chameleo* and *Brookia*, in which anconæus scapularis inserts on the posterior border of the scapula as in urodeles, while the scapulohumeralis arises from the posterior part of the girdle below it, just in front of the joint capsule, and the ligamentum also occupies a posterior position, acting as a second humeral ligamentous origin of anconæus scapularis.

Variations in the insertions, origins and muscular connections of ligaments and tendons is not surprising when one remembers that the skeleton is first laid down in connective tissue as localized in areas first of cartilage, then of bone. Thus in the humerus the shaft first forms in cartilage in a humeral tract preformed in mesenchyme, and in which the connective tissue areas are retained at the joints, to be finally invaded by cartilage, except where they articulate and except for the connective tissue which surrounds the joint and later becomes the capsule. Meanwhile bone replaces the cartilage of the shaft, but the latter is retained at the articulating surfaces, and the connective tissue remains as the membranæ intermusculares, the periosteum and the perimysium. All these connective tissue tracts offer opportunities both ontogenetically and phylogenetically for the developing muscles to seize as areas of origin and insertion, as well as aponeurotic connections. These areas are often specialized into ligaments and tendons, their points of attachment varying according to the mechanical necessities of the case, and occasionally forming bridges like the ligamentum scapulohumerale externum, to span invading muscles like the scapulohumerales. Probably if a careful comparative study of connective tissue areas were carried on in a series of types, correlated with a study of the musculature and skeleton, many of the puzzling problems of unusual muscle attachments could be solved.

(b) *Anconæus Humeralis Lateralis* (Figs. 19, 62, 63). This slip seems to be fairly constant in all types and there are no essential differences found in the comparison of *Megalobatrachus* and *Sphenodon*. Its lesser extent in the former is probably the result of aquatic habits.

(c) *Anconæus Humeralis Medialis* (Figs. 19, 65, 66). This slip also is clear in its homologies. It is the muscle of the dorsomedial surface and characteristically arises on an area extending from the joint capsule to a varying degree along the humerus, joining the common insertion from beneath. It is proportionally more extensively developed in *Sphenodon* than in *Megalobatrachus* for reasons similar to those in the case of the preceding slip.

(d) *Anconæus Coracoideus* (Figs. 65, 66). The homologies here are more puzzling than in any of the other slips, because of the position of the muscle with reference to inferior trunks from the brachial plexus. In *Sphenodon*, the entire N. brachialis inferior with its branches lies outside of and posterior to this slip, and thus to the entire anconæus muscle. In *Megalobatrachus*, the case is different. Though anconæus coracoideus arises from the posterior coracoidal angle, between the origins of Mm. subcoracoideus and coracobrachialis longus as in *Sphenodon* (Figs. 61, 65, 66), and inserts as the posterior division of the anconæus and in common with it on the proximal end of the ulna, it is nevertheless situated entirely outside the N. brachialis inferior, which passes between it and the other slips of the anconæus muscle. It also appears to be innervated near its origin by a small branch of the coracobrachialis nerve. This innervation and the fact that its fibres adjoin at their origin and are practically continuous with those of M. coracobrachialis longus, would indicate that in *Megalobatrachus* this slip is not homologous with the anconæus coracoideus of *Sphenodon*, but is rather a derivative of the M. coracobrachialis longus, to which it appears to be allied in innervation as well as in position. Its insertion, however, is clearly on the ulna in common with the anconæus, though at the most posterior part of the capsule not far from the distal fibres of the coracobrachialis longus insertion. If this diagnosis should prove to be correct, the anomalous insertion may be explained by a comparison with the condition in *Sphenodon*. Here the anconæus coracoideus has been reduced to a narrow strandlike tendon from the coracoidal origin throughout the greater part of its course. Near the insertion into the capsule, however, it expands into a thin fan-shaped muscular slip, which almost immediately enters the common insertion on the posterior part of the capsule, rising here above the level of the nerve complex. I would suggest that the tendinous part of this slip is derived from the connective tissue associated

with the immediately posteriorly situated nerve complex and with the posterior membrana intermuscularis; that the muscular slip has dwindled to its present distal position, but keeping its connection with the connective tissue, a portion of which became specialized as the tendon; that the muscular part is homologous only with the most distal fibres of the so-called anconæus coracoideus of *Megalobatrachus*, where they have been picked up by the proximal portion derived from the M. coracobrachialis longus, which thus constitutes by far the greater part of the slip. A muscle band is thus formed, occupying the position of a true anconæus coracoideus, so far as origin and insertion are concerned, but lying posterior to the N. brachialis inferior, and composed of a greater proximal coracobrachialis portion and a much smaller distal anconæal portion with an anconæal insertion.

This view needs further verification, but it is the only one which will explain the varying relationship to the N. brachialis inferior.

The condition in *Sphenodon* probably represents the ancestral condition, except that the slip was probably muscular throughout its whole extent. It is manifest that a slender tendinous band would not be as mechanically efficient for an animal the size of the larger stegocephs. In the restoration the anconæus coracoideus is therefore represented as a somewhat narrow muscular band forming a fourth slip of the anconæus mass.

Humeroradialis (Humeroantibrachialis Lateralis)

Figures 35, 40, 50, 52, 54, 70, 71

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> There is no muscle corresponding to that of <i>Sphenodon</i>. The ligamentum intermusculare, however, is here very strong and occupies the position of the M. humeroradialis of <i>Sphenodon</i>. It arises from the processus ventralis in close association with the deltoides system	<i>Origin</i> Ligamentum scapulohumerale laterale and from its tendinous continuation to the processus lateralis humeri. These origins are therefore associated with the processus lateralis and with the Mm. supracoracoideus and deltoides
<i>Insertion</i> The ligamentum intermusculare forms part of the origin of the M. supinator longus and is distally in continuity with the ectepicondyle	<i>Insertion</i> Superficially on the proximal part of the M. supinator longus and on the forearm fascia in close association with the ectepicondyle
<i>Innervation</i> No innervation, but the ligament connects an axillaris innervated muscle and a supinator innervated muscle	<i>Innervation</i> Proximally by a branch of the deltoides system; distally by a branch of the N. radialis lateralis (N. supinator)

This muscle is peculiar to *Sphenodon*. According to Fürbringer it does not exist in other lizards, but has a partial homologue in the crocodile and in birds. It is entirely lacking in Amphibia. As Fürbringer has pointed out (1900, pp. 496-497), it is in reality a compound muscle having a double innervation. The smaller proximal portion is a derivative of the *deltoides clavicularis*, as it is innervated by a branch of the same nerve. The greater distal portion is an offshoot of the *M. supinator longus* of the lower arm, innervated by a branch of the supinator nerve. The two portions are not visibly differentiated from each other, but together form a single long flat muscle band, arising partly from the *ligamentum scapulohumerale laterale* just distal to an insertion of the *M. supracoracoideus* on the more anterior part of the same ligament, partly from a tendinous continuation of the ligament which receives on its anterior side a part of the insertion of *M. deltoides clavicularis* (Fig. 54). It inserts on the proximal part of the *M. supinator longus* on its anterior edge.

In *Megalobatrachus*, and in urodeles generally, there is no muscle homologous with the *humero-radialis* as such, but, as indicated in the above table, the strong *membrana intermuscularis* of the anterior side of the limb runs along the same course from the deltoid region on the head of the humerus to the *ectepicondyle*, where it forms a large part of the origin of the most proximal slip of the *extensor carpi radialis* mass, shown below to be homologous with the *M. supinator longus* of reptiles. This would signify that on the reptilian branch the *Mm. supinator longus* and *deltoides clavicularis* extended their respective muscle areas along this membrane until they met to form the compound *M. humero-radialis*, in response to the greater demands of terrestrial life on the muscular apparatus of the limb, while on the amphibian side this did not take place. This is dealt with further in connection with the *M. supinator longus*.

The probable situation in *Eryops* can also be best understood after that muscle is discussed.

D. DORSAL MUSCULATURE OF LOWER ARM AND HAND

Supinator Longus

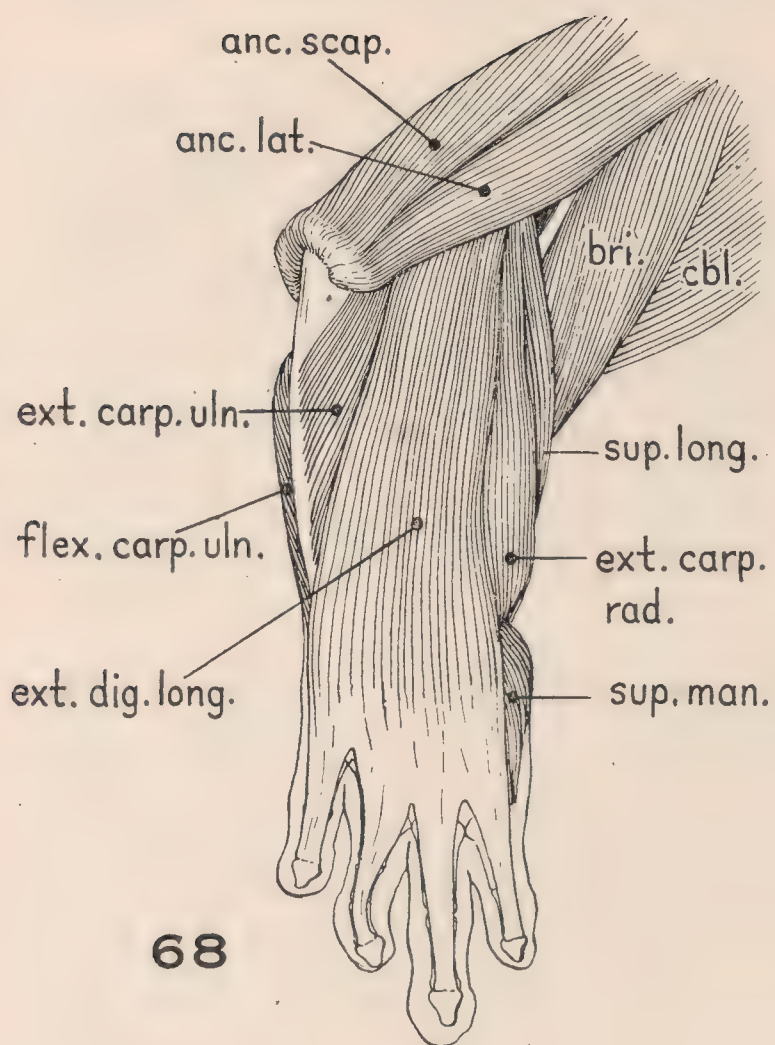
Figures 19, 51, 52, 68 to 71, 74, 77, 80

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Distal part of humerus on lateral angle, from ligamentum intermusculare and lateral surface of ectepicondyle	<i>Origin</i> Ectepicondyle and elbow-joint capsule beginning proximally to other exten- sor muscles
<i>Insertion</i> Radial side of radius near distal end	<i>Insertion</i> Radial side of radius near distal end
<i>Innervation</i> Branch of ramus radialis medialis of N. brachialis longus superior	<i>Innervation</i> Branch of ramus medialis of N. brachialis longus superior

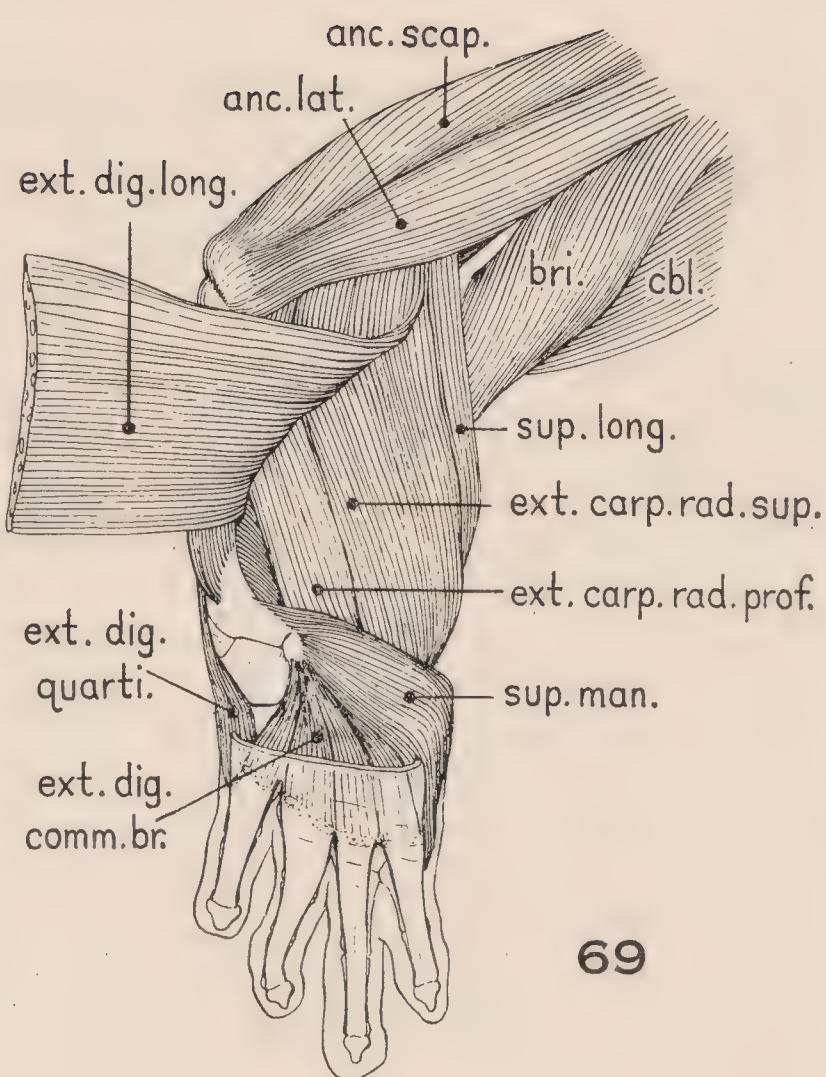
The salient ectepicondyle of the humerus is the place of origin for the extensor muscles of the lower arm, the most proximal of which in *Sphenodon* is the M. supinator longus. This arises both on the condyle itself and on the connective tissue adjacent to it, extending proximally for some distance along the supinator crest, which is quite prominent in *Sphenodon* (Figs. 18, 19, 20 F), as in reptiles generally. This origin is entirely lateral and proximal to the ectepicondylar foramen. It inserts on the radial side of the distal end of the radius.

In *Megalobatrachus*, Osawa (1902, pp. 280–281) considers the general extensor carpi radialis to be a single muscle, and does not differentiate a supinator. Humphry (1872, pp. 40–41) regards this mass as homologous to extensor carpi radialis brevis (superficialis), extensor carpi radialis longus (profundus), and supinator longus of reptiles. My dissection of *Megalobatrachus* (Figs. 44, 68, 69, 74) clearly shows a deeper proximal layer of this mass which is exactly in the position of M. supinator longus, arising from the ectepicondyle and especially from the ligamentum intermusculare, and which can be taken only as a supinator. It is innervated by a branch which may therefore be called the supinator nerve.

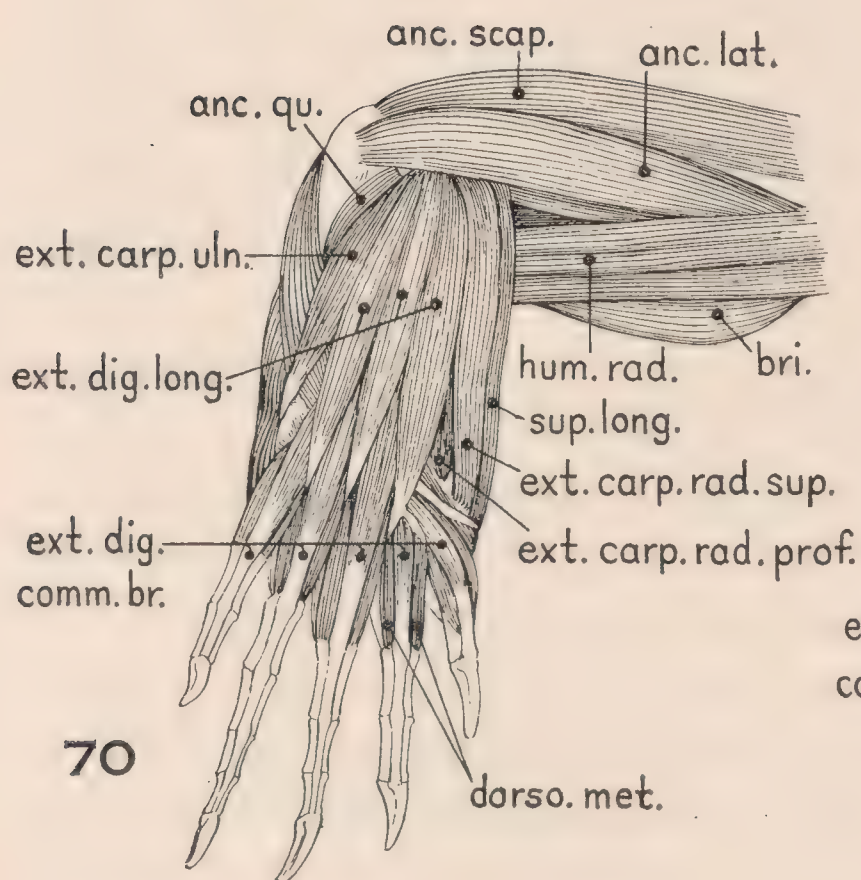
As stated in the section on the skeleton (p. 185), *Megalobatrachus* has no foramen through the ectepicondyle as in *Sphenodon*. In the latter animal, the ramus radialis medialis of the N. brachialis longus superior passes through this foramen. In *Megalobatrachus*, however, this nerve passes through the ligamentum intermusculare in just the position that



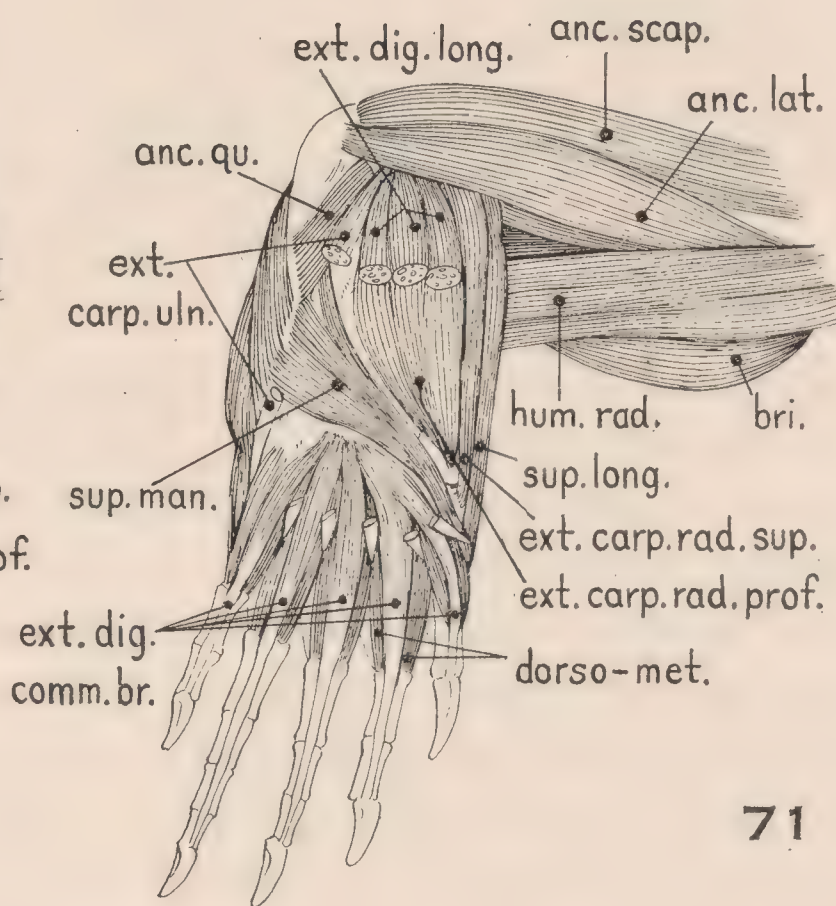
68



69



70



71

Fig. 68.—Dissection of the superficial extensor musculature of the forearm of *Megalobatrachus*.

Fig. 69.—Dissection of the deeper extensor musculature of the forearm of *Megalobatrachus*.

Fig. 70.—Dissection of the superficial extensor musculature of the forearm of *Sphenodon*.

Fig. 71.—Dissection of the deeper extensor musculature of the forearm of *Sphenodon*.

would be assumed by an ectepicondylar foramen, if the condyle had ossified out into the membrane to form a supinator crest including this part of the ligamentum. As the bone and cartilage are merely the ossified or chondrified portion of the original connective tissue membrane, the ligamentum intermusculare must be interpreted as that part of the original connective tissue which failed to ossify, and the part surrounding the medialis nerve is therefore an unossified supinator crest with its appropriate nerve penetration, and homologous to the ectepicondyle in *Sphenodon* with its foramen.

In *Eryops* (Fig. 20A), as shown on page 183, this foramen is incomplete, being indicated by a notch bounded by a prominent bony protuberance just proximal to the condyle. As already shown, this notch is also found in cotylosaur reptiles, and a series of fossil forms exhibits its gradual enclosure by an approximation of the projecting outer bone to the condyle until its distal end connects with the latter to form an ectepicondylar foramen (Fig. 20 A-E). It is evident that this enclosure took place around the medialis nerve and thus brought about the condition in modern reptiles (Fig. 20 F). In *Megalobatrachus* and the urodeles, on the other hand, the failure of complete ossification, due to aquatic specialization, left this foramen with its nerve out in the unossified membrane, with the result that the foramen is not found on the urodele humerus, and the nerve merely crosses the end of the bone without penetrating it. The condition in *Eryops* and the cotylosaurs is intermediate and ancestral to both extremes, with the notch functioning as an ectepicondylar foramen. The bony protuberance arose as a strong point of origin for the outer portion of the powerful extensor radialis muscle system necessary to lift the heavy body of *Eryops*, as the foot was planted on the ground. This outwardly projecting peg tended to separate the outer muscle slip to form a separate true supinator longus and apparently also acted as a point of insertion for part of the deltoid muscle or a prolongation from it, thus forming another fulcrum for the extensor system acting in connection with the deltoid. This extension of the latter muscle to this point was possible because of the short humerus and the consequent proximity of the deltoid crest. In fact, it is probable that a strong ligamentum intermusculare extended from this supinator crest to the neighboring deltoid crest, as in later forms. The configuration of the *Eryops* humerus shows a ridge (Fig. 20) connecting the two crests in exactly the position to be continued by a ligamentum intermusculare, as in later forms. In this case, it would be easy for the deltoid muscle to invade the dorsal surface of this ligament as a part of its inser-

tion. This process would bring it immediately into contact with the supinator crest, thus forming a M. humeroradialis inserting on the bony crest or protuberance. As this crest gradually swung parallel to the condyle in enclosing the foramen, as in the reptile stem, it would be drawn away from the primitive humeroradialis, leaving it to insert on the membrane near the M. supinator longus and finally on the muscle itself, as in *Sphenodon*. In the urodeles, on the other hand, there was a failure of ossification as an effect of aquatic habits, the “peg” deteriorated, the humerus elongated, the musculature became weaker, the supinator was left originating only from the distal end of the ligamentum intermusculare, while the weakening deltoid retreated to insert only on the processus ventralis, and, with the failure of the dermal cleithrum and clavicle and the resulting expansion of the cartilaginous procoracoid and supracoracoid expansions, divided to form the dorsalis scapulæ and procoracohumeralis muscles. Thus the ligamentum alone was left lying between the Mm. brachialis inferior and anconæus lateralis to connect the insertion of the deltoides system with the origin of the supinator, as in *Megalobatrachus*.

The restoration of the *Eryops* musculature thus requires a M. supinator longus arising from the projecting supinator crest, and a M. humeroradialis inserting on this same crest and on the ligamentum intermusculare connecting the two crests (Figs. 80, 103).

Extensor Carpi Radialis Superficialis (Brevis)
Figures 19, 69 to 71, 74, 77, 80

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Distal part of ligamentum intermusculare laterale humeri and from lateral surface of the ectepicondyle	<i>Origin</i> From the lateral side of the ectepicondyle and from the elbow-joint capsule distal to origin of M. supinator longus
<i>Insertion</i> Radiale and radial part of centrale	<i>Insertion</i> On distal end of radius close to that of M. supinator
<i>Innervation</i> Branch of ramus radialis medialis from N. brachialis longus superior	<i>Innervation</i> Branch of ramus radialis medialis of N. brachialis longus superior

This muscle, the extensor carpi radialis brevis of Osawa, is more appropriately to be termed the extensor carpi radialis superficialis, both because of its more superficial position with respect to the other radialis muscles and because it is longer than the "longus" (page 257).

In *Sphenodon* (Figs. 19, 70, 71, 77), it arises from the ectepicondyle just distal to the supinator longus and inserts on the distal end of the radius also in close proximity to that muscle.

In *Megalobatrachus* (Figs. 19, 69, 74), a similar muscle is clearly homologous, though it inserts on the radiale and centrale. However, the insertion in *Sphenodon* in my dissection is so near the radiale that it may well be a variable matter. Osawa says (1898, p. 562) that in *Sphenodon* it unites with an aponeurosis which inserts on the proximal end of metacarpus I. This is not the case in my dissection.

In *Eryops* (Fig. 80), because of the strong ectepicondyle, this muscle must have been comparatively powerful and inserted on the large radiale and perhaps also on the expanded distal end of the radius.

Extensor Carpi Radialis Profundus (Longus)

Figures 19, 69, 71, 74, 77, 80

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Distal part of ectepicondyle adjoining origin of M. extensor carpi radialis superficialis	<i>Origin</i> Distal part of ectepicondyle and from elbow joint distal to origin of M. extensor carpi radialis superficialis
<i>Insertion</i> Almost the entire length of the radius, the membrana interossea and on the intermedium	<i>Insertion</i> Distal half of the radius and on membrane inserting on radiale and membrane of wrist
<i>Innervation</i> By short nerve from plexus anti-brachialis, i.e., from both rami radiales medialis and lateralis of N. brachialis longus superior	<i>Innervation</i> By branches from both rami radiales medialis and lateralis of N. brachialis longus superior

This muscle as shown above is quite clear in both *Sphenodon* and *Megalobatrachus*. The origin is similar, and, while the insertion varies somewhat in the two forms, it is largely associated with membranous tracts, which, as we have seen, are notoriously variable.

The innervation is exactly homologous, though in *Megalobatrachus* the two nerves unite in an antibrachial plexus before entering the muscle, while in *Sphenodon* they enter it without forming a plexus.

This was doubtless a very important muscle mass in *Eryops* (Fig. 80), the large overhanging surface of the ectepicondyle giving it a strong attachment, while the widely expanding distal end of the radius furnished it with a large triangular facet for insertion, with a very direct pull. The intermedium is also in an excellent position to receive a part of the insertion, which also, perhaps, invaded the centrale. The small interval between the radius and ulna speaks for a small attachment on an interosseous membrane, and, therefore, together with the wide bony area for insertion, implies that the muscle was exceptionally powerful.

As this muscle is comparatively short, Osawa's term "longus" is scarcely descriptive. As it is situated more deeply than the preceding muscle, I have thought it well to give it the name "profundus."

Extensor Carpi Ulnaris

Figures 19, 68 to 72, 75, 78

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> With Mm. extensores carpi radialis and digitorum longus from point of the ectepicondyle and the fascia between it and the M. extensor digitorum longus	<i>Origin</i> From surface of ectepicondyle in common with the other extensors
<i>Insertion</i> Ulnar border of ulna, and slightly on ulnar side of ulnare	<i>Insertion</i> Distal end of ulna, on pisiform, and on ulnar side of metacarpus V, near joint with phalanx
<i>Innervation</i> Ramus radialis lateralis from N. brachialis longus superior	<i>Innervation</i> Ramus radialis lateralis from N. brachialis longus superior

The origin, insertion and innervation of this muscle in *Megalobatrachus* and *Sphenodon* sufficiently attest its homology in both urodele and reptile branches. It is interesting to note that, in reptiles, its insertion generally extends not only to the distal end of the ulna, but also to the pisiform and to metacarpus V. In urodeles, however, in correlation with the loss of digit V, its insertion is more proximal, and on

the ulna only or at most slightly on the ulnar side of the ulnare. The fibres also insert more obliquely toward the outer edge of the ulna in urodeles than in reptiles where the course of the muscle is more parallel with the ulna. In other words, in reptiles the muscle is associated with the fifth digit in its insertion, while in urodeles it tends in a sense to run off the arm before it reaches the hand, as if directed toward the vanished fifth digit.

The "anconæus quartus," or more properly "quintus" (Osawa) (Figs. 19, 70, 71, 75), is a small slip from this muscle arising from the end of the ectepicondyle in common with it and inserting on the ulnar border proximal to the insertion of the main muscle. In *Megalobatrachus*, there is but a single muscle mass, homologous to both slips.

In *Megalobatrachus* (Fig. 72), also, the muscle arises from the fascia between it and the M. extensor digitorum longus. In fact, all the extensor muscles arising from the ectepicondyle tend to be more unified into a single mass at their origin in urodeles than in reptiles.

In *Eryops* (Fig. 78), the extensor carpi ulnaris was doubtless a single muscle. Because of the four-fingered condition of the *Eryops* hand, it is represented as inserting on the outer border of the ulna, on the ulnare, and the pisiform, extending down to the rudimentary cartilage at the outer distal end of the ulnare, the existence of which is indicated by a facet at that point, as shown in figures 21, 78 to 80.

Extensor Digitorum Longus

Figures 19, 68 to 71, 73, 76, 79

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Ectepicondyle and the fascia between it and the M. extensor carpi ulnaris	<i>Origin</i> Ectepicondyle and the elbow-joint capsule in common with the other extensors
<i>Insertion</i> Divides into four tendinous slips which insert on the dorsal aponeuroses of the respective fingers	<i>Insertion</i> Splits on back of hand into four muscular slips which insert on ulnar side of bases of metacarpals I-IV
<i>Innervation</i> Short rami musculares from the plexus antibrachialis and thus from both rami radiales lateralis and medialis from N. brachialis longus superior	<i>Innervation</i> Rami lateralis and medialis of the radialis system from N. brachialis longus superior

In *Sphenodon* (Figs. 19, 70, 71, 76), this muscle arises as a powerful extensor from the ectepicondyle between the Mm. extensores carpi radialis and ulnaris. It soon divides into three slips which insert on the ulnar side of metacarpals II, III, IV. A slip for the ulnar side of metacarpale I arises from the distal part of that inserting on II. Each insertion is by a delicate tendon alternating with the five slips of M. extensor digitorum communis brevis, the origin of which is covered by this muscle.

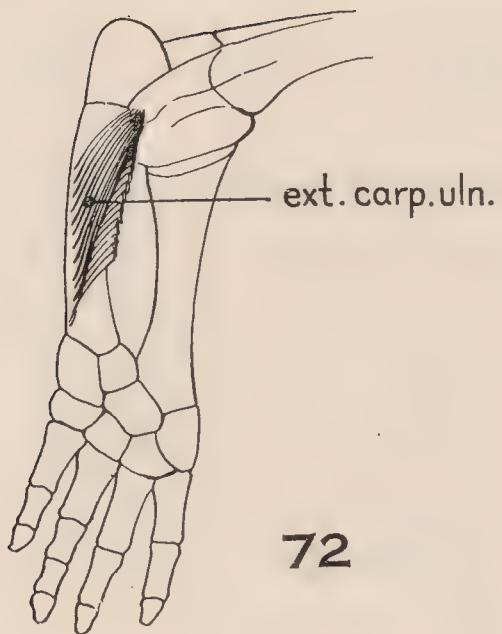
In *Megalobatrachus* (Figs. 19, 68, 69, 73), the origin is broader and thinner than in *Sphenodon*, in fact almost aponeurotic. This muscle passes as a single layer distally to the region of the carpus. Here it becomes aponeurotic and divides to form four flat tendinous slips, each of which passes dorsally over its appropriate digit to insert at the base of a terminal phalanx. On the under side of each slip at its base, there is an insertion of one of the four muscular slips of extensor digitorum communis brevis.

It is evident that the two sets of muscles form homologous systems in the two animals. The muscular slips of extensor digitorum communis brevis in *Sphenodon* end in tendons which insert on the terminal phalanges. The homologous slips in *Megalobatrachus* are continuous, from beneath, with the four tendinous slips into which the M. extensor digitorum longus is described as dividing. As a matter of fact, the latter muscle merely extends to the wrist and then inserts on the surface of the brevis at the beginning of its tendons, instead of remaining separate and inserting on the metacarpals between them as in *Sphenodon*. Hence, so far as the M. extensor digitorum longus is concerned, its special homology merely extends to that part of the musculature extending from the origin on the ectepicondyle to the wrist.

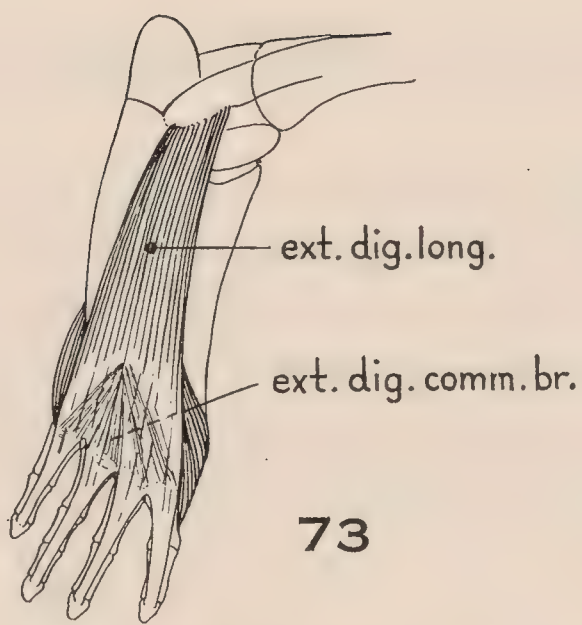
It appears to have been originally the superficial portion of the distal part of the general extensor muscle mass which inserted on the outer connective tissue membranes of the wrist, and thus belongs particularly to the lower arm musculature, as distinguished from the muscles of the hand. In *Sphenodon*, it continues to hold its original relations, but has specialized, having evolved four slips and four tendinous insertions on the bases of the metacarpals. This is a terrestrial specialization.

In *Megalobatrachus*, the main muscle mass, as in the majority of urodeles, inserts on the wrist aponeurosis, which in turn receives from beneath the insertions of the four slips of the underlying brevis muscle.

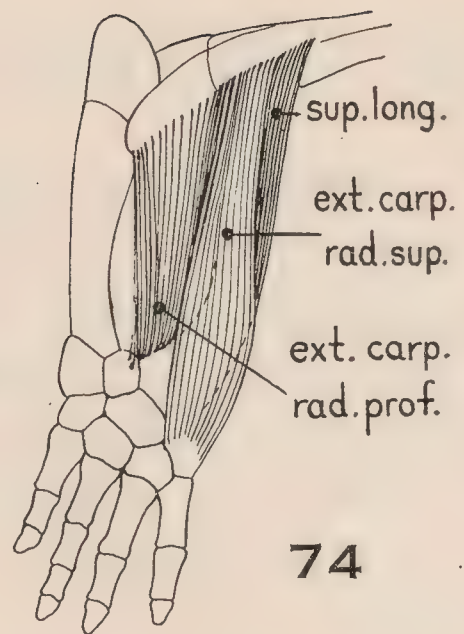
Though *Megalobatrachus* is specialized for aquatic life, I believe this insertion on the dorsal aponeurosis to be more primitive than the condi-



72

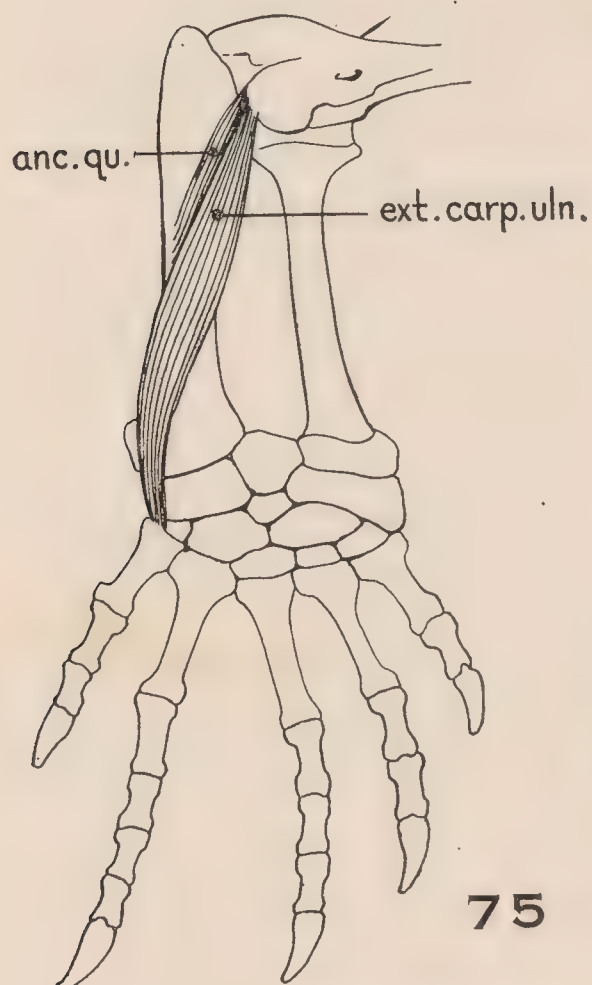


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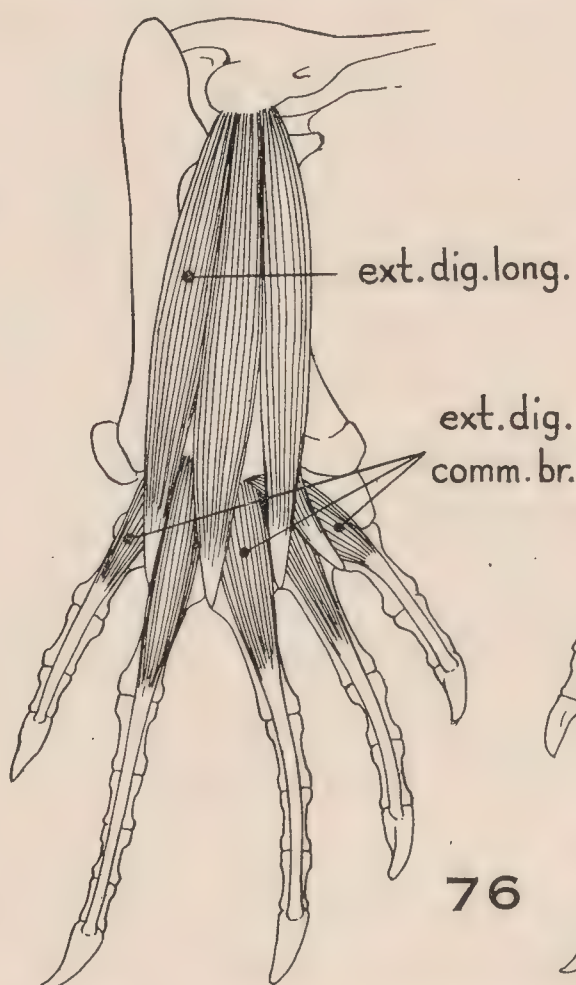


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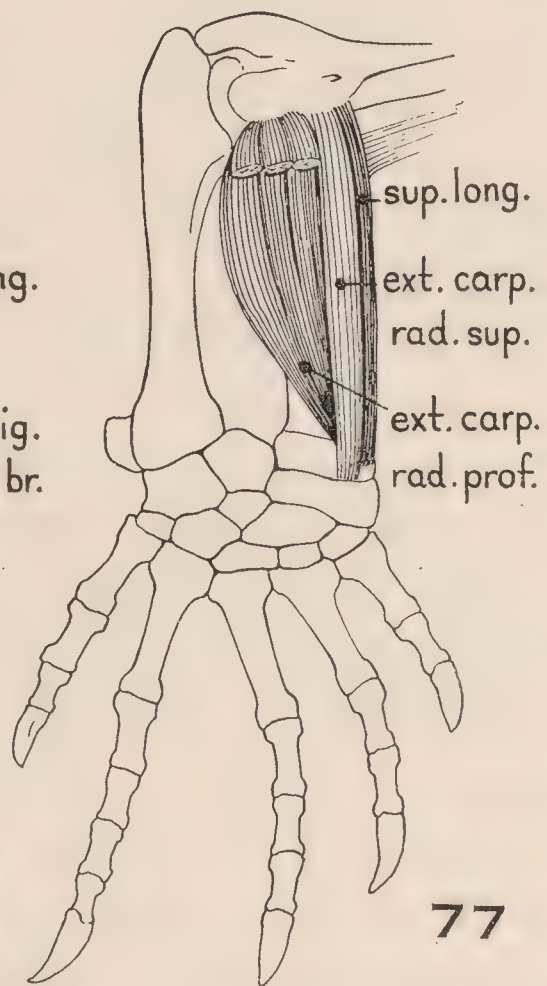
Megalobatrachus



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76

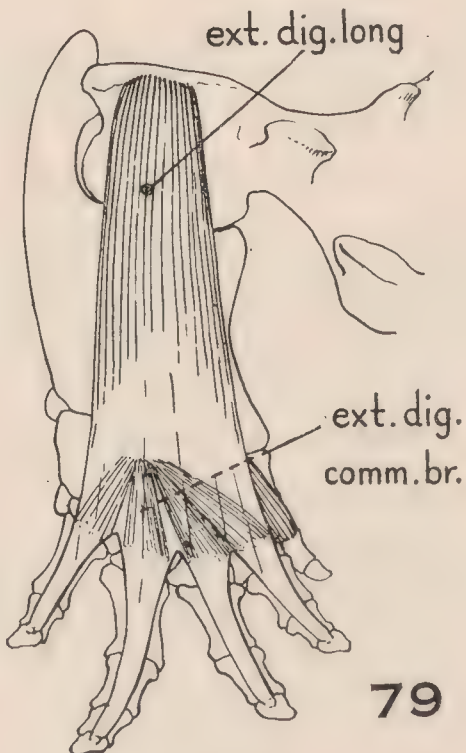


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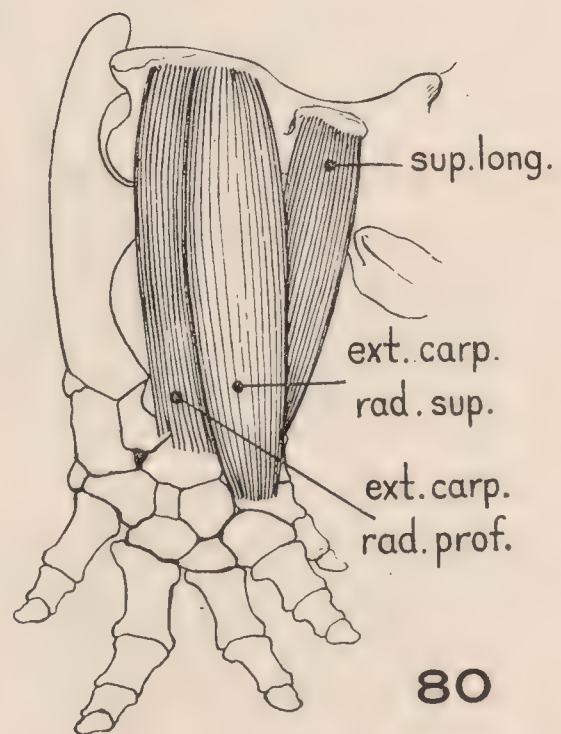
Sphenodon



78



79



80

Eryops

Figs. 72 to 80

tion in *Sphenodon*. As the primitive muscle mass penetrated the hand and the fingers, the superficial layers apparently first inserted on the superficial connective tissue, from which they appropriated strips in the direction of the pull to become separated out as tendons. The inferior layers and the origins, on the other hand, became connected with the bone through the intermediary of the perimysium, the periosteum and the intervening connective tissue. As the muscle invaded the finger elements, the lower surface found an attachment on the phalanges, and the upper surface on the under side of the tendinous strips. The mechanical pull would naturally cause these to be situated obliquely with regard to one another, so that the skeletal connection would be situated proximally in the hand and distally in the fingers with reference to the respective connections with the tendons.

In *Eryops* (Fig. 79), therefore, I am inclined to assign to this muscle a condition more nearly resembling that of *Megalobatrachus*, but with stronger tendons, as indicated by the heavy ulnar prolongations of the proximal ends of the metacarpals (Fig. 21) and by the more or less terrestrial habits of the animal.

Supinator Manus (Abductor et Extensor Pollicis Longus)

Figures 69, 71

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Distal end of ulna on its radial border and from intermedium	<i>Origin</i> Outer side of distal part of ulna and from the ligamentum intermusculare
<i>Insertion</i> After a diagonal course across the wrist it inserts on the fascia of the radial border of the wrist and on the base of metacarpal I on its dorsal side	<i>Insertion</i> After a diagonal course across the wrist it inserts on the radial border of the wrist and on the dorsal aponeurosis of digit I
<i>Innervation</i> Ramus dorsalis manus intermedius from plexus radialis antibrachii, which is formed by rami radiales lateralis and medialis from N. brachialis longus superior	<i>Innervation</i> Nn. radiales medialis and lateralis from N. brachialis longus superior

Figs. 72, 75, 78.—Comparison of M. extensor carpi ulnaris in *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*.

Figs. 73, 76, 79.—Comparison of Mm. extensor digitorum longus and extensor digitorum communis brevis in *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*.

Figs. 74, 77, 80.—Comparison of the radioextensor muscle system in *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*.

In *Sphenodon* (Fig. 71), this muscle has a widespread origin on the distal half of the ulna and from the membranous area between it and the radius.

In *Megalobatrachus* (Fig. 69), the origin is much more compressed, arising merely from the radiodistal end of the ulna and from the intermedium. It is to be noticed, however, that the origin is generally ulnar in character and is closely associated with the common origin of the M. extensor digitorum communis brevis, together with which it combines in a fan-shaped system to the hand.

In both animals, it takes a diagonal course across the carpus and inserts on the radial side of the wrist-capsule. In both cases, it pulls on the radial side of the base of the first metacarpal and hence has an influence on the first digit, for which it thus acts as an extensor as well as for a general abductor for the carpus. The point to bear in mind is that it has a general ulnar origin and yet an insertion on the radial side of the carpus. This is to be considered in connection with the following muscle.

The innervation in both forms is homologous. As the homologies are so clear, this muscle must have been well defined in the Stegocephalia, and hence is represented in *Eryops* as a part of the fundamental hand musculature.

The abductor et extensor pollicis longus is termed the abductor digiti secundi in *Megalobatrachus* by Osawa (1902, p. 283), on the theory that the first digit has disappeared in urodeles. As it has been clearly demonstrated by recent workers that the fifth digit has disappeared and that the first is still present in these forms, Osawa's terminology is faulty in this respect, and the muscle should have the same name as its homologue in *Sphenodon*.

Extensor Digitorum Communis Brevis
Figures 69, 71, 73, 76, 79

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Radial part of ulnare and from inter-medium	<i>Origin</i> Distal radial corner of ulnare and from intermedium
<i>Insertion</i> Ventral side of aponeurotic slips of M. extensor digitorum longus, where they enter the digits I, II, III and IV	<i>Insertion</i> Immediately forms five slips to fingers I to V, respectively, where they terminate as tendons inserting on the bases of the terminal phalanges
<i>Innervation</i> Rami dorsales manus intermedius and ulnaris as well as ramus dorsalis manus radialis, the two former from plexus antibrachii formed by Nn. radiales lateralis and medialis, and the latter from N. radialis superficialis, all from N. brachialis longus superior	<i>Innervation</i> Ramus medialis of N. radialis from N. brachialis longus superior

Osawa (1902, p. 284) states that the origin of this muscle in *Megalobatrachus* includes the radiale, ulnare and three radial carpalia. In my dissection (Fig. 69), the origin is shown clearly as the radial part of the ulnare and the intermedium. After careful examination, I could find no trace of origins from either radiale or carpalia. As this corresponds exactly with the condition in *Sphenodon*, I feel certain that Osawa is mistaken. Again, Osawa (1898, p. 566) mentions only four slips as belonging to this muscle in *Sphenodon*, inserting on digits II to IV respectively. In my dissection, a fifth slip similar to the other four goes quite conspicuously to end as a tendon on the terminal phalanx of digit I, arising in common with the other four, as shown in figure 71.

In *Megalobatrachus* (Figs. 69, 73), the terminal tendons of these muscles unite with the aponeurosis of M. extensor digitorum longus to insert on the terminal phalanges, while, in *Sphenodon*, this does not take place, since the slips of the latter muscle, as mentioned above (page 259), insert on the ulnar side of the bases of metacarpales I to IV (Figs. 70, 71). This condition in *Sphenodon* is a terrestrial adaptation which apparently arose in the following way.

M. extensor digitorum longus is a muscle belonging to the lower arm rather than to the hand. This is shown by the fact that its muscular mass is situated entirely in that region and inserts into the aponeurosis of the wrist. M. extensor digitorum communis brevis is a carpal muscle, arising from carpal bones only, and inserting into the dorsal aponeuroses of the phalanges. The former mass, therefore, derived its tendinous termination from the wrist, while the latter derived its five tendons from the fingers. The muscular action of the fingers in terrestrial locomotion would naturally tend to keep them independent of the arm muscle in action, while its primitively single sheetlike tendon would eventually split through the action of the contracting finger muscles, remaining attached only between the slips. In *Megalobatrachus*, however, because of its swimming method of progression, the limb would move as a whole and the fingers would not be subject to independent stress and action; hence their musculature would become relatively unimportant, while the pressure of the paddlelike action would affect the hand and arm as a unit. In this case the broad aponeurotic insertion of the extensor digitorum longus would act most effectively in connection with the hand as a whole, while the brevis connection would be weakened and subordinated to it. This condition is realized in the *Megalobatrachus* hand, the paddlelike action of which is further assisted by the broad skin flanges on the sides of the flat fingers.

Interossei et Abductor Pollicis Brevis (Dorsometacarpales and Extensor Digiti Quarti)
Figures 69 to 71

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> The only representative of this series is apparently the M. extensor digiti quarti ("quinti" of Osawa), which arises on the distal end of the ulna, and runs down the ulnar side of the fourth metacarpal (considered the fifth by Osawa) No muscles on I to III	<i>Origin</i> Including the abductor pollicis brevis, these are ten little muscles, which, excepting the above, arise from the bases of the respective metacarpals, in pairs, on either side the digit. The abductor pollicis brevis arises from the radiale. Otherwise it corresponds to interosseus on the ulnar side of the thumb
<i>Insertion</i> Dorsal aponeurosis of fourth or ulnar-most finger No muscles on I to III	<i>Insertion</i> Basal phalanx of each finger in pairs on radial and ulnar sides respectively, then fusing with dorsal aponeurosis
<i>Innervation</i> As in preceding muscle	<i>Innervation</i> As in preceding muscle

These muscles should be treated as a unit, and as a whole might better be called in *Sphenodon* the "dorsometacarpales," as they lie along the dorsal side of the metacarpal bones. They have the same innervation as the extensor digitorum communis brevis and are evidently the deeper slips of the same muscle system. The radial muscle of digit I has extended its origin to the radiale. As it is on the outside of the digit, this results in its acting as an abductor. There is also a tendency for the ulnar slip of digit V to encroach proximally to derive its origin from the carpus. The development of these slips is correlated with terrestrial habits.

In *Megalobatrachus*, on the other hand, there exists the usual lack of development to be expected in an aquatic animal. There being no independent stress on the digits, no deeper muscles of this series appear except on the ulnar side of digit IV, where a well-developed slip arises from the ulna, called by Osawa the "extensor digiti quinti proprius." As, however, there is no fifth digit, it should rather be known as the "extensor digiti quarti proprius" (Fig. 69). The innervation is the same as in *M. extensor digitorum communis brevis*, and should be classed as a deeper element of that system, like the corresponding muscle in *Sphenodon*.

As *Eryops* had a powerful and well-developed carpus and more or less terrestrial habits, a system of metacarpal muscles somewhat like those of *Sphenodon* would be necessary, as a part of the dorsal extensor system of the hand.

E. THE EXTENSOR ARM MUSCLES IN GENERAL

The extensor system of the upper arm consists of the four anconæus muscles which unite in a single insertion on the proximal end of the ulna, thus transmitting all extensor pulls and stresses to that element of the skeleton. This extensor muscle group is continued to the lower arm by the series of extensors arising from the ectepicondyle of the humerus, which is therefore the extensor condyle. This series acts as a brake on the flexor system in lowering the hand to the ground. The muscles arising from the distal part of the condyle insert on the ulna and on practically the entire carpus. These are the extensor carpi ulnaris and the extensor communis digitorum longus, and are continued into the hand by the supinator manus, the extensor digitorum communis brevis, and the dorsal finger muscles generally. On the contrary, the muscles arising from the proximal part of the ectepicondyle and inserting on the radius, together with the similar set on the flexor side and the anconæus system

of the upper arm, are those most effective in lifting the hand from the ground from its backward position, preparatory for the forward reach. They are the *extensores radiales superficialis* and *profundus* and the *supinator longus*.

Thus it will be seen that the muscle arrangement corresponds with the bones of the lower arm and the hand. All the digits radiate from a pyramid of carpal bones including all but the radiale as shown by Gregory (1915, pp. 363–364). The apex of this pyramid is formed by the intermedium and ulnare, which together support the ulna. Thus the most powerful extensor muscles converge on the ulna from the upper arm, while, in the manus, it is evident from figure 71 that practically all the extensor muscles of the hand and fingers diverge from the ulna and the ulnar pyramid of carpal bones. The proximal muscles, on the other hand, converge from the supinator crest and the proximal part of the condyle to the radius and radiale and seem to run off the hand on the radial border. As shown by Gregory, Miner and Noble (1923), the comparative anatomy of the reptile and amphibian skeleton, supported by embryological indications, clearly proves the former existence of a prepollex in the ancestors of these groups, articulating from the radial series of bones, namely, the radius, radiale and mediale. The latter element may have disappeared in the adult modern form, but was clearly evident in the *Eryops* carpus (Fig. 21).

The course of the radial musculature in *Megalobatrachus* inserts on this series. This consideration, and the fact that it does not enter into the musculature of any of the five surviving digits where they exist, are strong evidence that these muscles are the survival of a prepollical musculature. In the reconstruction of *Eryops* they are made to converge to that element. The evidence of the musculature thus supports, as well, the thesis of Gregory and others regarding the ulnar pyramid and the arrangement of the primordial rays of the hand. Likewise, the insertion in *Sphenodon* of the *M. extensor carpi ulnaris* on the pisiform, and its ulnaroblique course and insertion on the ulna itself, suggest the former existence of a postminimus element, of which it appears to be vestigially the former musculature. It thus confirms, from the point of view of musculature, the proofs from embryology along the same line (see Gregory, Miner and Noble (1923)).

It is also noteworthy, in *Megalobatrachus*, and other urodeles which have lost both digit V and the postminimus, that the *M. extensor carpi ulnaris* inserts on the ulna in a more proximal position than in five-fingered forms like *Sphenodon*, and is directed toward the ulnar border by

a wider angle, as would be expected if its course were aimed at two lost digits instead of one.

F. VENTRAL MUSCULATURE OF LOWER ARM AND HAND

Palmaris Communis Superficialis

Figures 19, 81 to 84, 86, 89, 92

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Entepicondyle of the humerus in common with Mm. flexores carpi radialis and ulnaris	<i>Origin</i> Entepicondyle of the humerus and elbow-joint capsule in common with Mm. flexores carpi radialis and ulnaris
<i>Insertion</i> Forms broad aponeurosis at wrist into which the M. palmaris profundus inserts from dorsal side and which then divides into five tendinous slips, one of which inserts on the radial side of metacarpal I, and the rest insert on the bases of the terminal phalanges of digits I to IV	<i>Insertion</i> Forms broad aponeurosis at wrist, which is joined dorsally by M. palmaris profundus and then splits into five tendons which insert on the terminal phalanges
<i>Innervation</i> Ramus superficialis medialis of N. brachialis longus inferior	<i>Innervation</i> Ramus superficialis medialis of N. brachialis longus inferior

While the homologies of this muscle are clear, as the origins, insertions and innervations correspond in urodeles and reptiles, nevertheless its relations to the Mm. flexores breves sublimis have been complicated by the fact that in the hand region its aponeurosis in reptiles is spanned on the ventral side by the aponeurosis of the latter muscles, while in urodeles it lies superficially. This particular feature will be dealt with under the heading of the Mm. flexores breves sublimis (p. 281 ff).

The palmaris communis superficialis [palmaris superficialis, Mc-Murrich, Wilder; flexor digitorum communis profundus of *Sphenodon*, Osawa; flexor digitorum longus sublimis of *Megalobatrachus* (*Cryptobranchus*), Osawa; flexor sublimis digitorum, Humphry; epitrochleo-ulno-digitalis, Fürbringer; flexor digitorum profundus, Günther; flexor primordialis communis, Ribbing] occupies the greater part of the superficial palmar aspect of the hand. It always arises from the entepicondyle as a muscular sheet which inserts into the palmar aponeurosis, which in

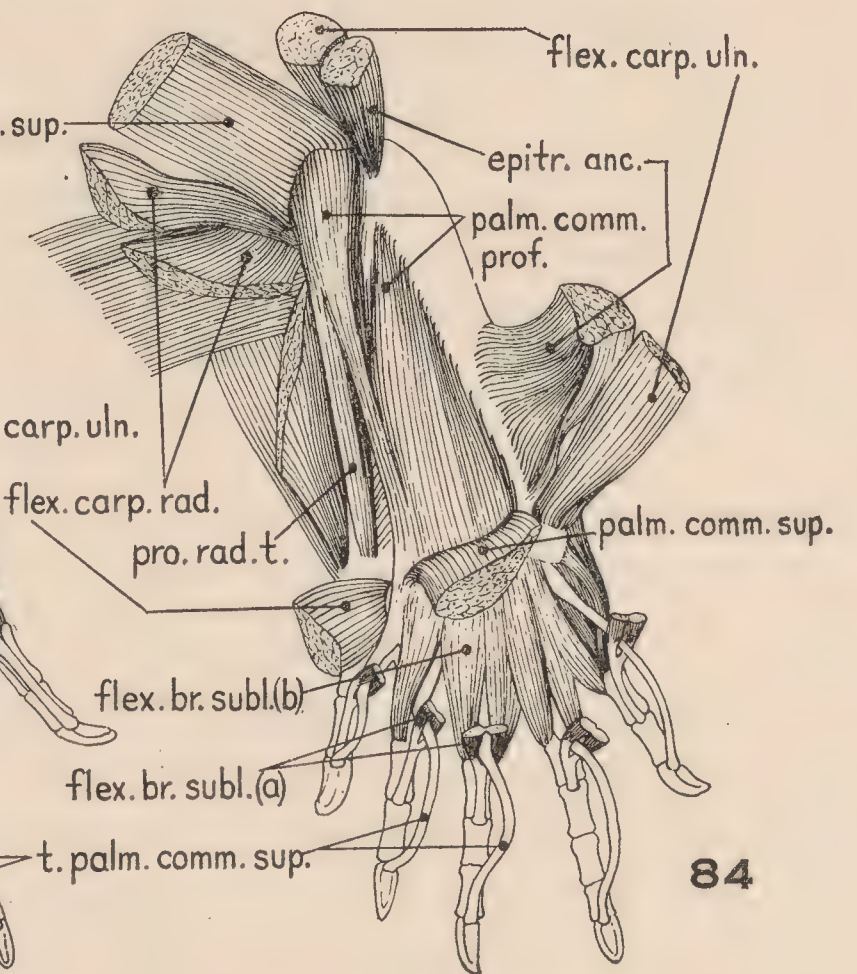
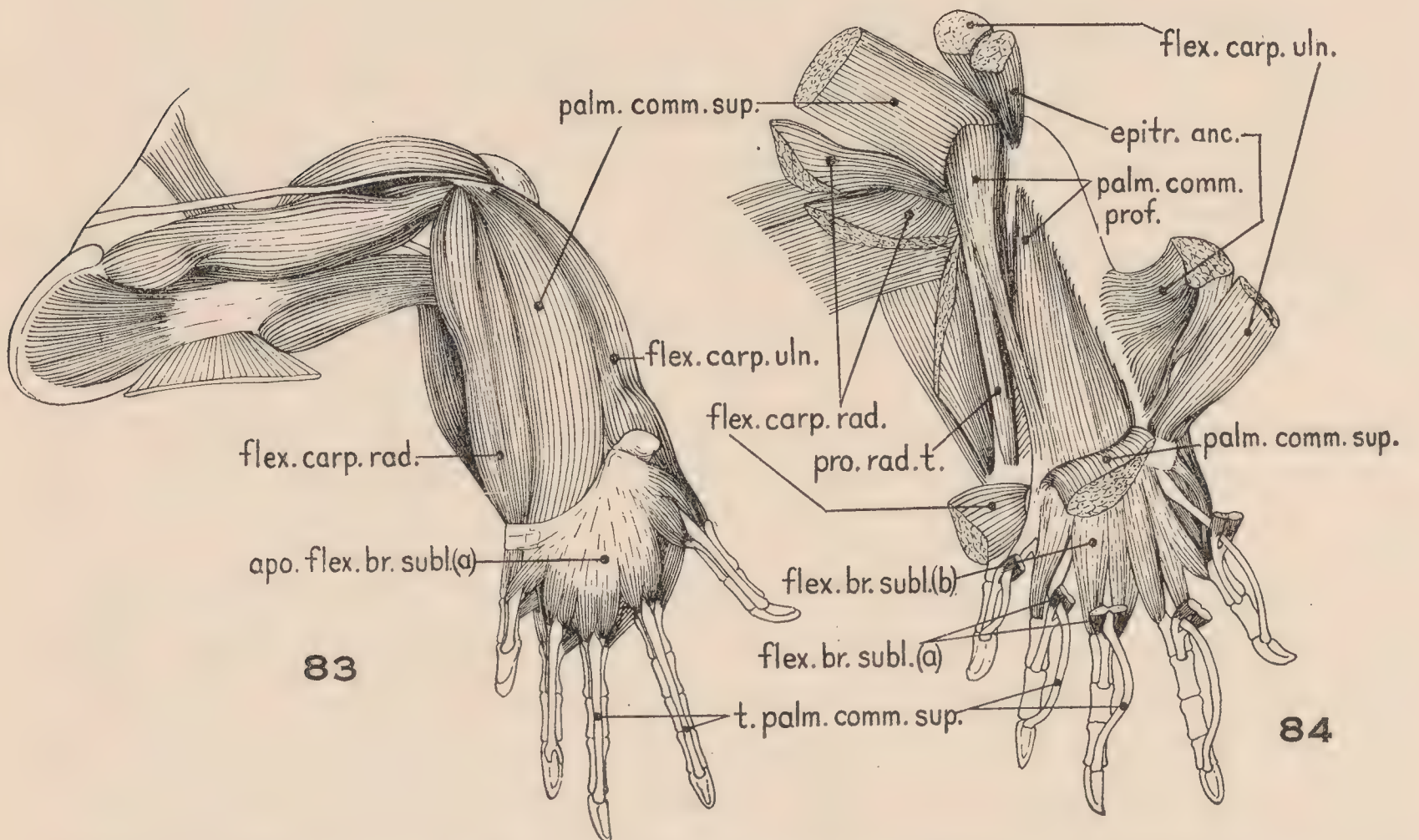
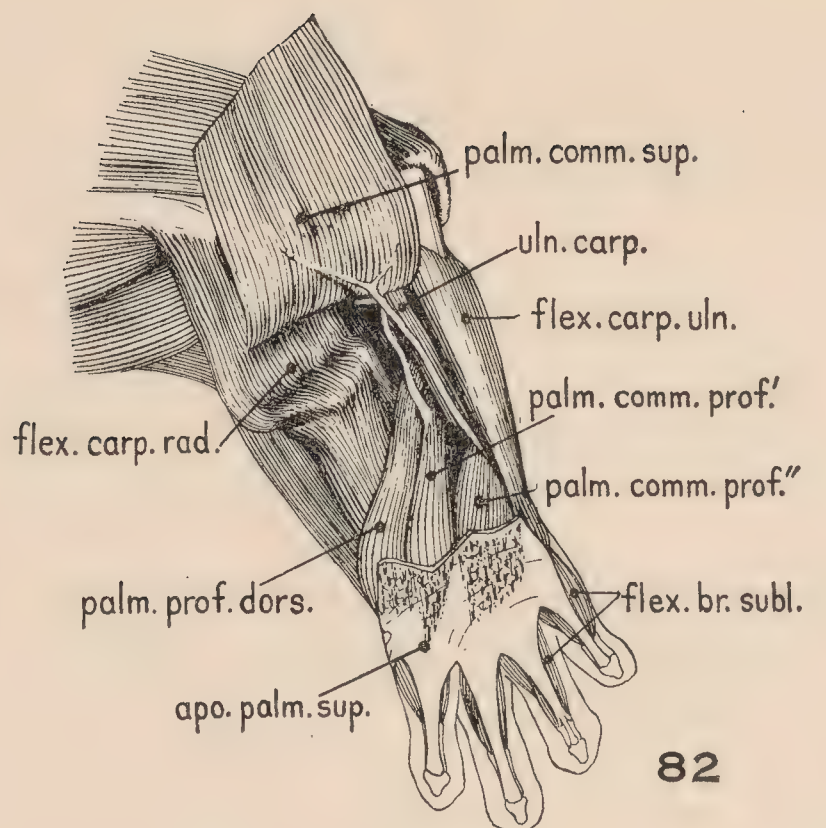
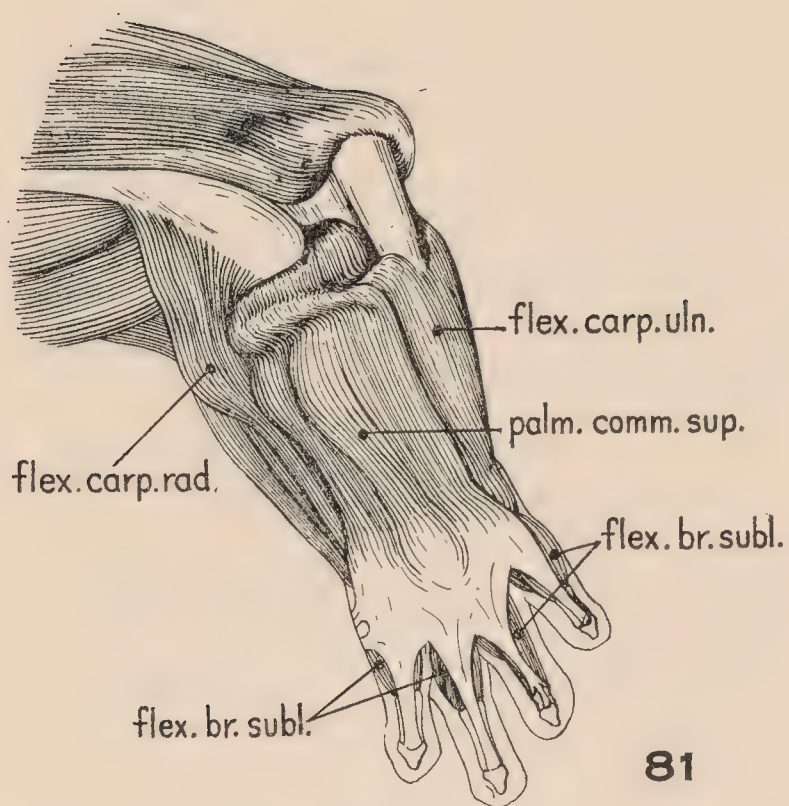


Fig. 81.—Dissection of the superficial flexor musculature of the forearm of *Megalobatrachus*.

Fig. 82.—Dissection of middle layer of flexor muscles in the forearm of *Megalobatrachus*.

Fig. 83.—Dissection of the superficial flexor musculature of the forearm of *Sphenodon*.

Fig. 84.—Dissection of the middle layer of flexor muscles in the forearm of *Sphenodon*.

turn splits into tendinous bands inserting on the terminal phalanges. It thus corresponds to the extensor digitorum longus of the dorsal side of the hand.

In *Megalobatrachus* (Figs. 81, 82, 86), as there are but four digits, there are four slips extending along the phalanges. A fifth slip is also present, inserting on the radial margin of the first metacarpal, perhaps a rudiment of a former connective tissue slip to the vanished prepollex.

In *Sphenodon* (Figs. 83, 84, 89), the muscular portion is more powerful and fleshy than in *Megalobatrachus*, as would be expected in view of its terrestrial habits.

The innervation is by the medial branch of the ramus superficialis of the brachialis inferior, the same ramus that innervates all the more ulnar muscles.

In *Eryops* (Fig. 92), a muscle of the same general type, common to both forms, is to be inferred, but inclined to the more powerful type characteristic of *Sphenodon* and the lizards generally. There would be four well-developed tendons, as in urodeles, and perhaps a small tendon to the prepollex, indicated by the rudimentary fifth slip of *Megalobatrachus*. It is possible, however, that this rudiment is merely a fascial carpal support to strengthen the wrist, since the prepollex doubtless had its own independent radial musculature.

Palmaris Communis Profundus

Figures 19, 82, 84, 86, 89, 92

MEGALOBATRACHUS	SPHENODON
<i>Origin</i>	<i>Origin</i>
(a) Ventral head From ulnar border of ulna near distal end	(a) Distal head From distal three-fourths of ulna
(b) Dorsal head From radial part of the distal half of ulna, separated from above by M. ulnocarpale	(b) Proximal head From proximal surface of ulna just beneath the joint capsule, and under the origin of M. palmaris communis superficialis
<i>Insertion</i>	<i>Insertion</i>
Both heads insert on the dorsal side of the aponeurosis of M. palmaris communis superficialis, (a) being situated to the ulnar side of (b), which inserts between it and the insertion of M. palmaris profundus dorsalis	Both heads insert in common into the proximal end of the palmar aponeurosis immediately beneath the junction of M. palmaris communis superficialis with it
<i>Innervation</i>	<i>Innervation</i>
Ramus superficialis medialis of N. brachialis longus inferior	Ramus superficialis medialis of N. brachialis longus inferior

In both *Megalobatrachus* and *Sphenodon*, three deep muscle heads arise from the ulna and insert on the dorsal side of the palmar aponeurosis of the palmaris communis superficialis. Two of these are innervated by the same nerve as that muscle, the ramus superficialis medialis, while the third is innervated by a different nerve, the ramus profundus. The latter head, the palmaris profundus dorsalis, will be treated later (page 279), as it belongs to a different series. The two former heads, grouped together as the palmaris communis profundus, because of their innervation, must also be related to the superficial muscle, of which in reality they form the deeper layer.

In *Megalobatrachus* (Figs. 82, 86), the two heads are separated by the M. ulnocarpalis, which passes between their ulnar portions. The course of these muscles is diagonal and parallel, one being located ventral to the other, as shown in the above table. Both insert on the dorsal side of the palmar aponeurosis, the dorsal head having an insertion radial to the ventral head.

The relations in *Sphenodon* (Figs. 84, 89) are similar, except that no M. ulnocarpalis is present; the two heads arise from the ulna, one from a greater distal origin, and the other from a lesser proximal origin; their course is at the same depth, and their fibres join before insertion. The insertion also appears to enter the proximal end of the aponeurosis rather than its dorsal side, sharing this feature with the muscular fibres of the M. palmaris communis superficialis which enter immediately ventral to the insertion of the former.

A similar condition must have existed in *Eryops* (Fig. 92), as these muscles are found in both lines of descent from the common stegocephalian ancestry. There was probably a closer resemblance to the urodele condition, hence a M. ulnocarpalis is postulated.

Pronator Radii Teres

Figures 84, 89, 98

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> No muscle of this name, but the deeper radial fibres of M. palmaris communis superficialis are homologous with it	<i>Origin</i> Entepicondyle of the humerus, beneath and radial to the origin of M. palmaris communis superficialis
<i>Insertion</i> None	<i>Insertion</i> Lower part of the radial side of the radius
<i>Innervation</i> None	<i>Innervation</i> Ramus superficialis medialis of the N. brachialis longus inferior

In *Sphenodon*, there is another deep muscle head of the same series as the preceding, as shown by the innervation, the M. pronator teres. It arises in common with the proximal head of the M. palmaris communis profundus, but from the lower and under part of the entepicondyle. It diverges from the palmaris, however, and inserts on the distal part of the radius.

In *Megalobatrachus*, there is no muscle of this nature, and this probably represents the more primitive condition, since the pronator is obviously a radial derivative of the deeper palmaris musculature.

In *Eryops*, we must postulate the more primitive condition, hence no separate M. pronator radii teres is inferred.

Flexor Carpi Ulnaris

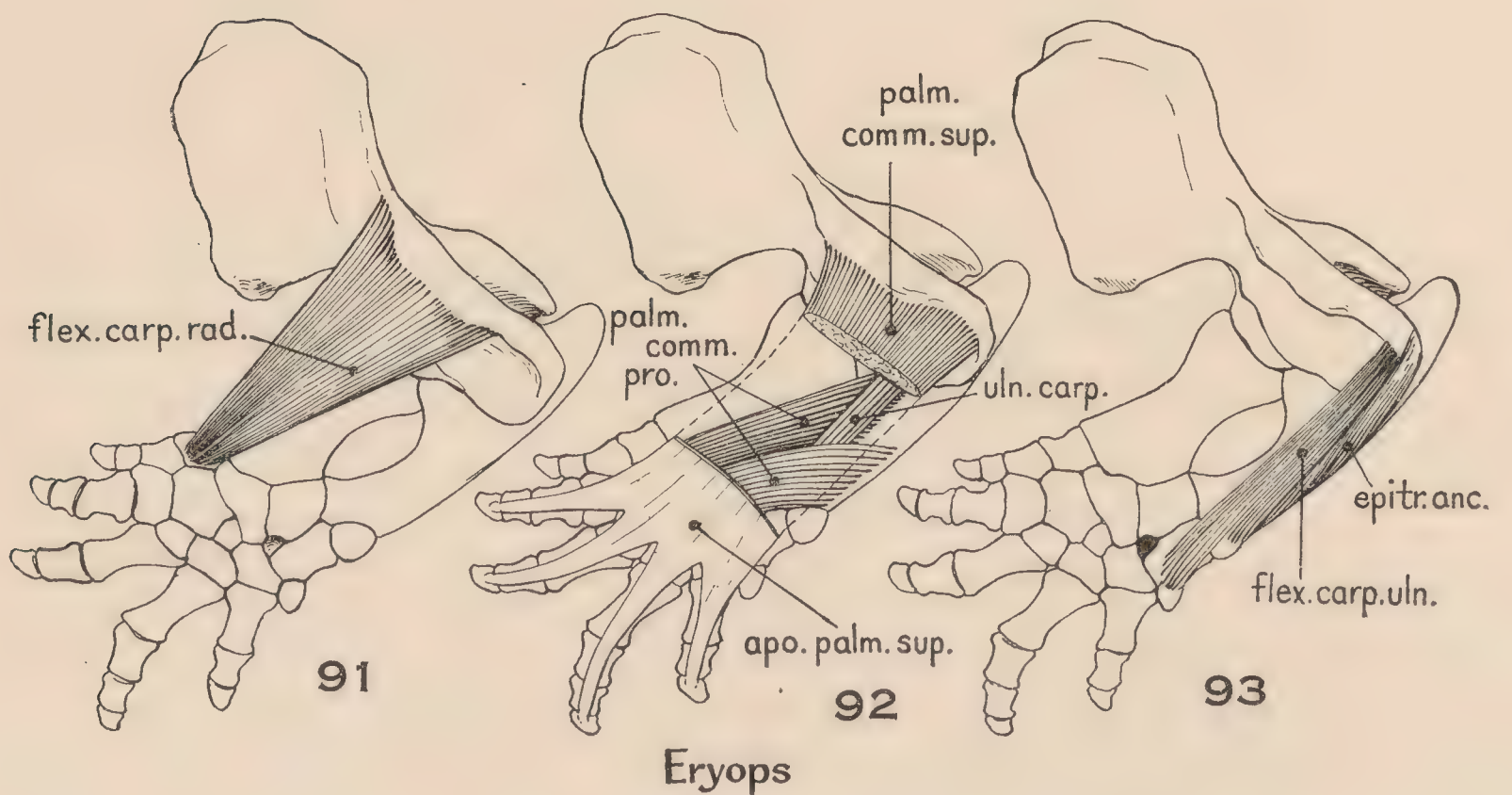
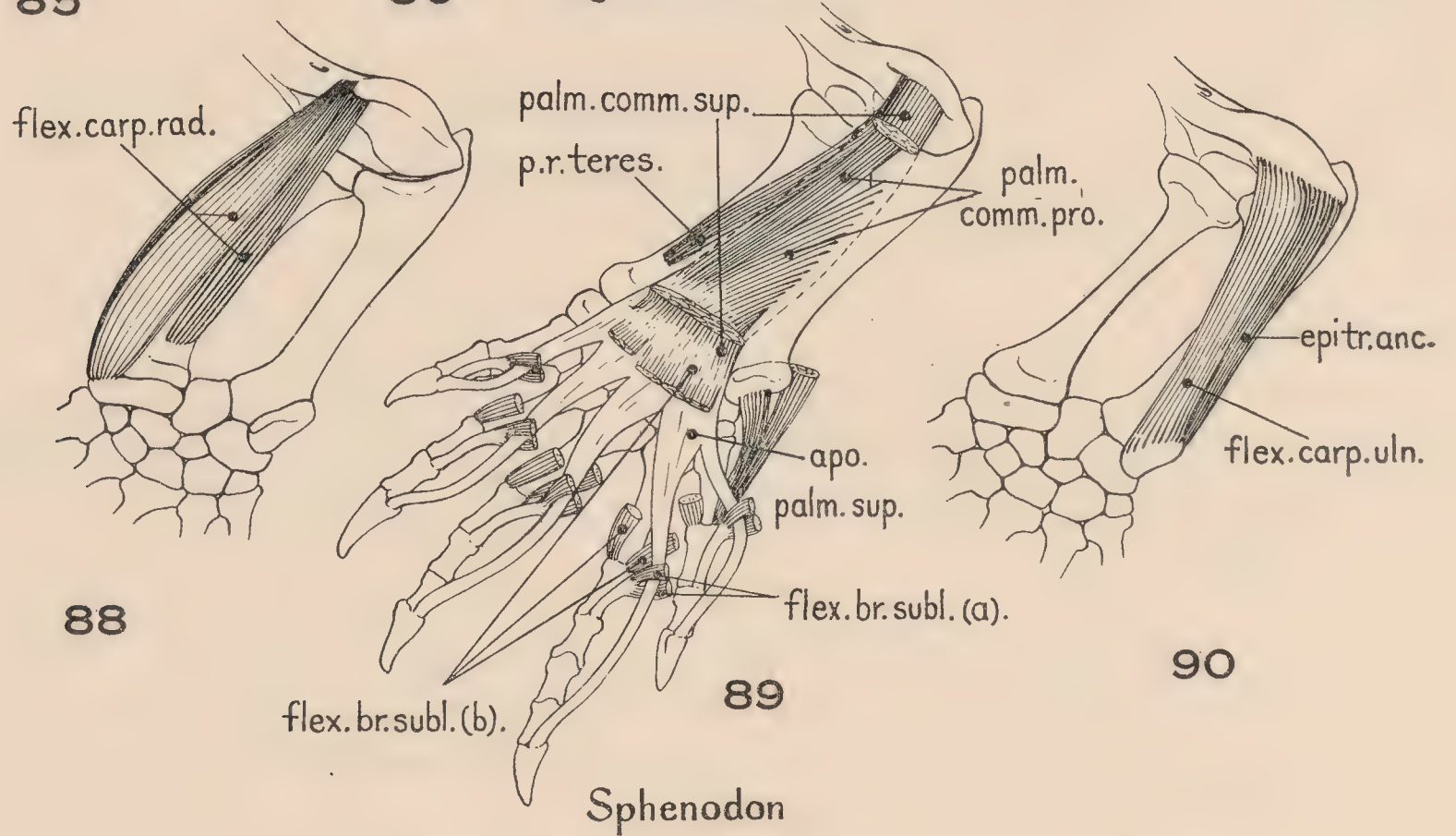
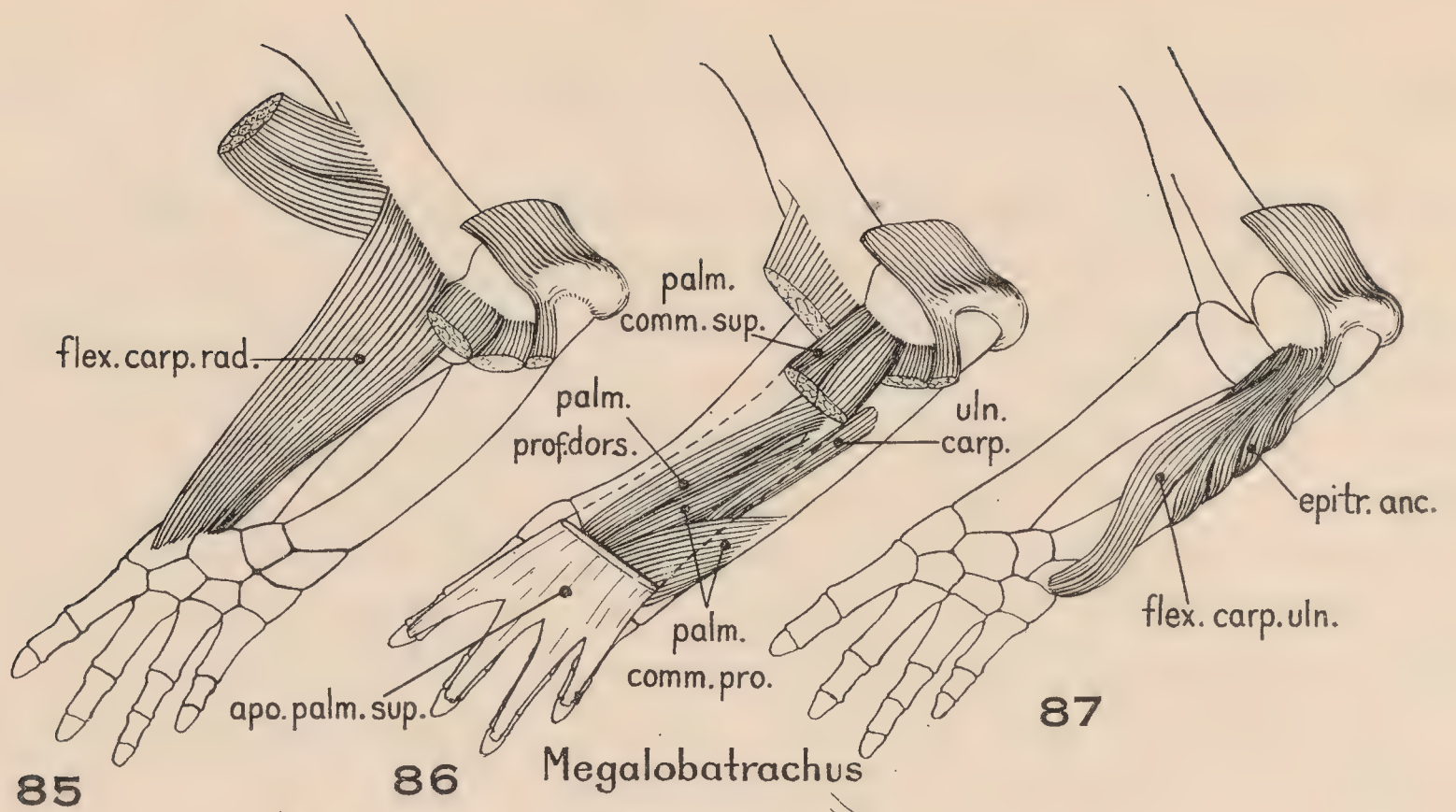
Figures 19, 81 to 84, 87, 90, 93, 98

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> From distal end of entepicondyle of the humerus distal to M. palmaris superficialis and proximal to M. epitrochleoanconæus	<i>Origin</i> From entepicondyle of the humerus between Mm. palmaris superficialis and epitrochleoanconæus
<i>Insertion</i> On flexor and ulnar surfaces of ulnare and on tendinous arch which gives rise to carpometacarpales	<i>Insertion</i> On flexor surface of pisiform
<i>Innervation</i> Ramus superficialis ulnaris of N. brachialis longus inferior	<i>Innervation</i> Ramus superficialis ulnaris of N. brachialis longus inferior

This muscle and the Mm. epitrochleoanconæus and ulno-carpalis also form a related series, as shown by their common innervation by the ramus superficialis ulnaris of the N. brachialis longus inferior. The first two are found in both urodeles and reptiles, but the latter only in urodeles.

The flexor carpi ulnaris arises in both *Megalobatrachus* and *Sphenodon* from the distal end of the entepicondyle, adjacent to the M. palmaris communis superficialis, and between it and the M. epitrochleoanconæus.

In *Megalobatrachus* (Fig. 87), it inserts on the ulnar part of the ulnare as well as on the tendons of the wrist. In *Sphenodon* (Figs. 84, 90), it inserts on the pisiform alone. As it seems to be clear that the latter



Figs. 85 to 93

element is the base of a vanished sixth digit, the ulnaris may possibly have been part of the musculature of that digit.

Epitrochleoanconæus
Figures 19, 84, 87, 90, 93

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Distal end of entepicondyle and capsule of elbow joint	<i>Origin</i> Distal end of entepicondyle and capsule of elbow joint
<i>Insertion</i> Median one-third to one-half of ulnar border of ulna	<i>Insertion</i> Distal end of ulna on ulnar border
<i>Innervation</i> Ramus superficialis ulnaris of N. brachialis longus inferior	<i>Innervation</i> Ramus superficialis ulnaris of N. brachialis longus inferior

This is really a more distal portion of the preceding muscle, but is nevertheless separate in both urodeles and reptiles. It arises in both *Megalobatrachus* and *Sphenodon* from the most distal portion of the entepicondyle, distal to the origin of M. flexor carpi ulnaris, and inserts on the ulnar border of the ulna. In *Megalobatrachus* (Fig. 87), this insertion is on the middle part of the ulna, while in *Sphenodon* (Fig. 90) it is on the distal part. As on the extensor side (page 266), this may be significant, as in the urodeles two digits are lost, the minimus and postminimus, while in reptiles the postminimus only is lacking. On both sides of the carpus, therefore, the ulnar musculature “runs off” the arm at a higher point in urodeles than in lizards.

As both ulnar muscles are present in both groups, they are presented as separate muscles with similar relations in *Eryops* (Fig. 93). As seen in the discussion of the manus of *Eryops* (page 188), there are clear indica-

Figs. 85, 88, 91.—Comparison of M. flexor carpi radialis in *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*.

Figs. 86, 89, 92.—Comparison of Mm. palmaris communis superficialis, palmaris communis profundus and ulnocarpalis, in *Megalobatrachus* and *Sphenodon*, with especial reference to their relations to the aponeurosis palmaris superficialis, and their inferred restoration in *Eryops*.

Figs. 87, 90, 93.—Comparison of the Mm. flexor carpi ulnaris and epitrochleoanconæus in *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*.

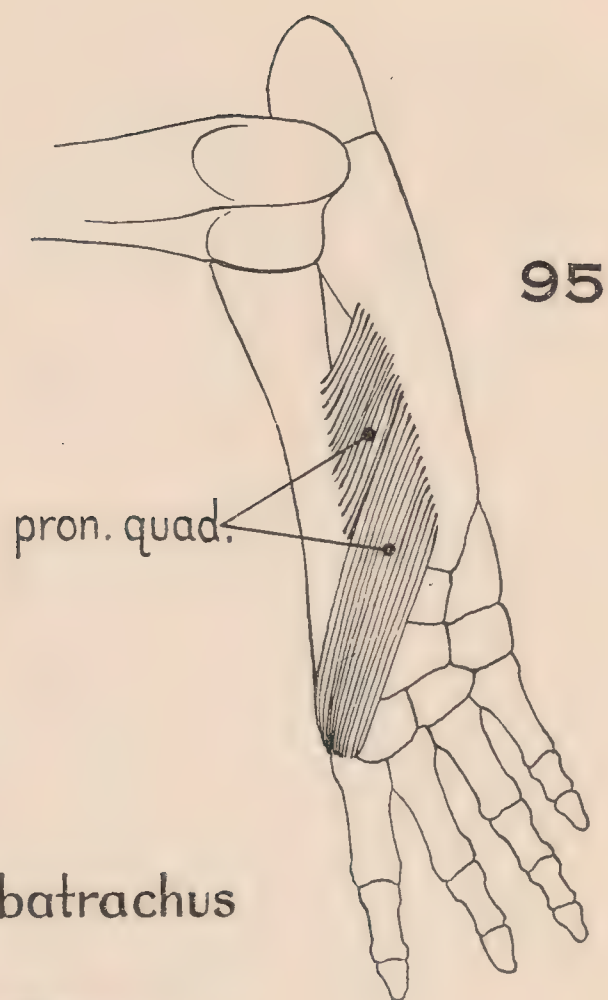
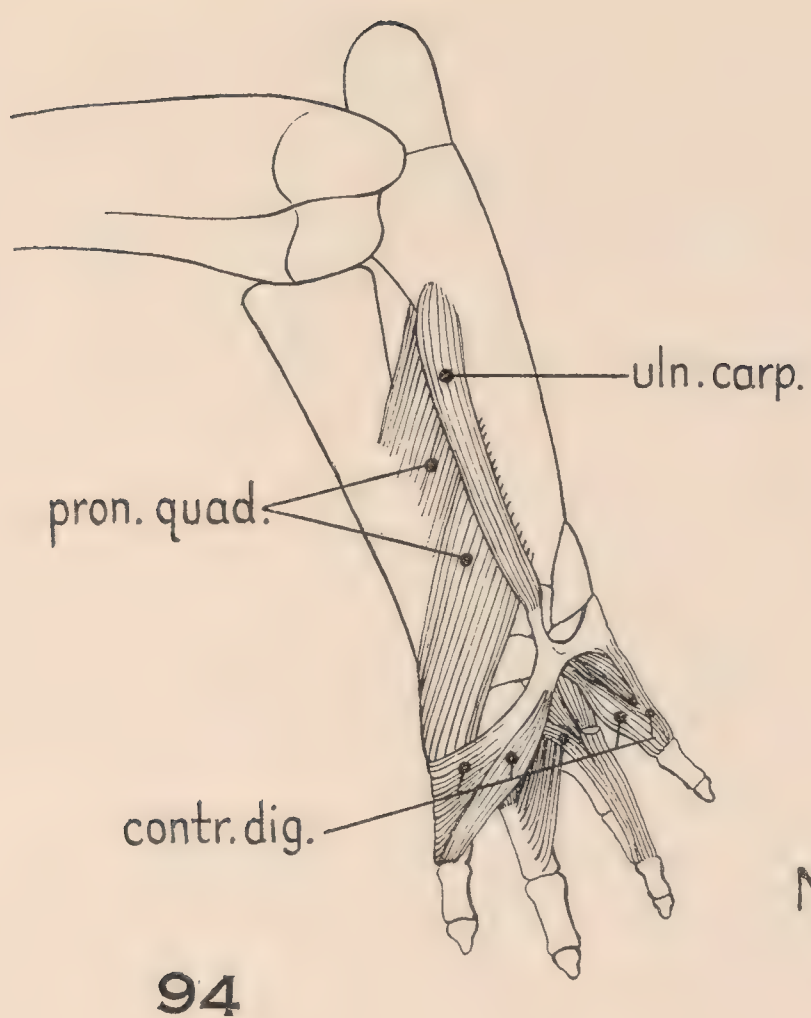
tions on the ulnar side of the fossil carpus of articular surfaces for both minimus (digit V) and pisiform (digit VI), to which this musculature is directed.

Ulnocarpalis
Figures 82, 86, 92, 94, 100

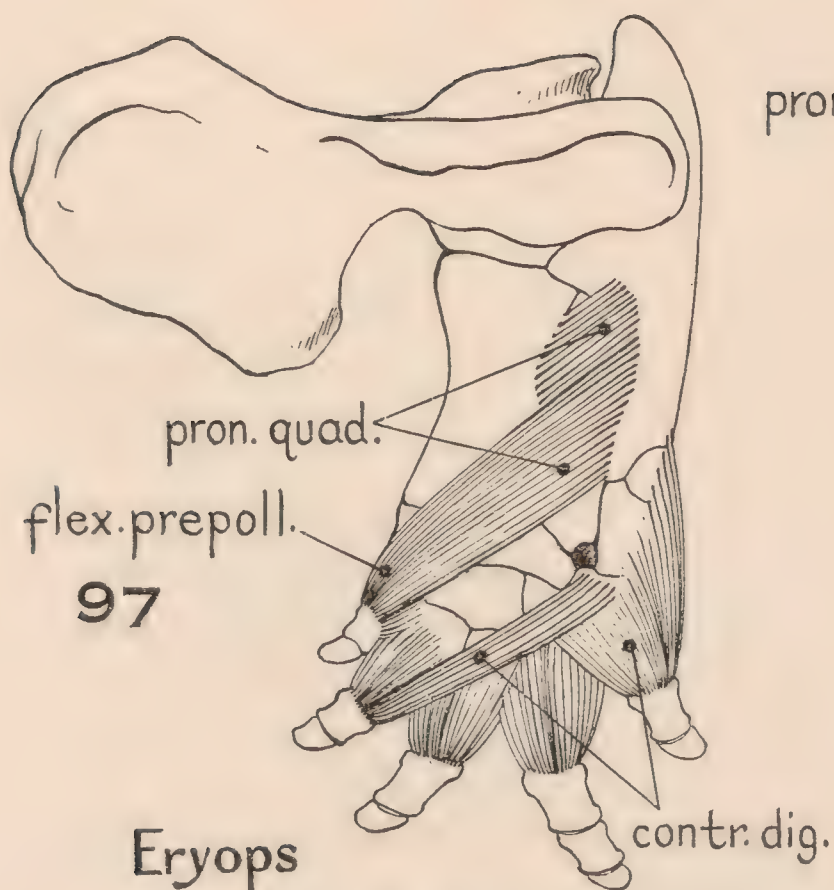
MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Proximal half of radial surface of ulna	<i>Origin</i> None
<i>Insertion</i> Delicate tendon inserts on tendinous bridge which forms origin of contrahentes digitorum	<i>Insertion</i> None
<i>Innervation</i> Ramus superficialis ulnaris of N. brachialis longus inferior	<i>Innervation</i> None

This purely urodele muscle is present in its typical condition in *Megalobatrachus* (Fig. 94). It arises on the proximal half of the ulna and inserts by means of a much attenuated tendon on a delicate and very deeply situated palmar bridge connecting the most ulnar elements of the deep finger musculature with the most radial elements of the same series. It is said by McMurrich (1903, p. 179) to insert on the distal carpal bones in *Amblystoma* and *Plethodon*. Wilder (1912, p. 402) gives its insertion in *Necturus* as carpalia 4 and 5. Osawa¹ (1902, p. 279) states for *Megalobatrachus* (*Cryptobranchus*) that it inserts partly on the base of metacarpale V, and partly as a tendinous band as far as the base of metacarpale II. Ribbing's investigation agrees most nearly with mine, although he is not explicit. He says (1907, pp. 624-625) that this muscle distally fastens itself with a fan-shaped spreadout tendon to some of the carpal pieces. From this tendon, as well as from the same carpal pieces, arise the Mm. flexores digitorum. The union between these flexors and the M. ulnocarpalis, he says, is most intimate in *Siredon* and *Amblystoma*, and least intimate in *Menopoma*. I have made a most careful dissection of this muscle, shown in figure 100, and I have found that the "tendinous bridge" wraps itself around the ulnar side of carpale IV and gives off a muscle slip to the ulnar border of metacarpale IV.

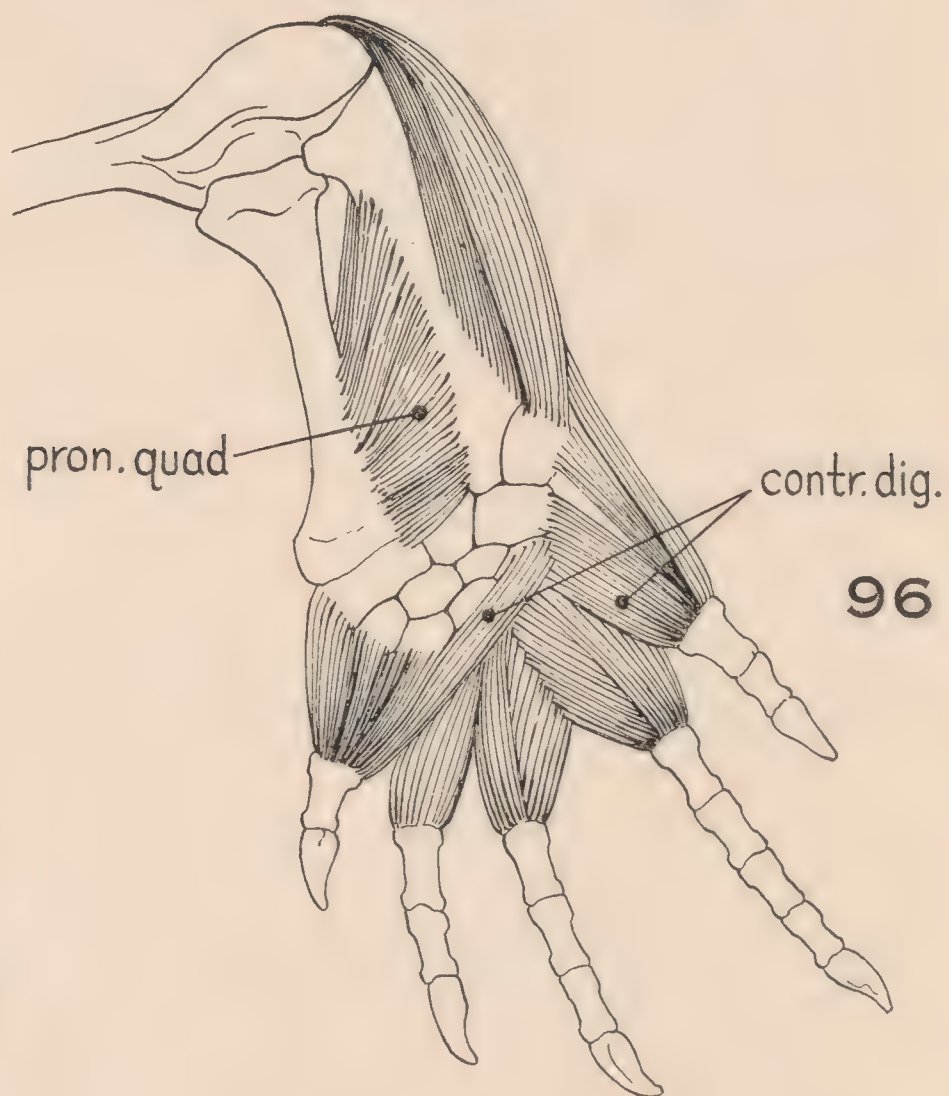
¹Osawa calls this muscle the "flexor profundus longus."



Megalobatrachus



Eryops



Sphenodon

Figs. 94, 95, 96, 97.—Dissection and comparison of the deepest layer of forearm muscles and the Mm. contrahentes digitorum of *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*.

It then passes transversely across the hand to terminate in one of the Mm. contrahentes digitorum, which inserts on the radial border of metacarpale I. During its course, it receives the insertion of M. ulnocarpalis at the junction of carpale IV with the centrale, but arching freely over both. The tendon of M. ulnocarpalis seems to be practically continuous (through the membrane of the bridge at its junction with it) with the origin of a muscle slip of the contrahentes system inserting on the radial side of metacarpale IV. I agree with Ribbing's suggestion that the M. ulnocarpalis was formerly continuous with the deeper finger flexors, and formed one muscle with them in ancestral types, thus making the deepest layer of the general ulnar muscle complex, as distinguished from the purely radial musculature of the ancestral prepollex, now remaining as the musculature of the radius and radiale.

In *Eryops* (Fig. 92), this musculature was doubtless more important, since it is in a degenerate condition in modern urodeles, and to this primitive condition *Megalobatrachus* gives an intermediate clew. Hence in the restoration of *Eryops* with its heavier demands on all elements of the limb muscles, we may picture an ulnocarpalis arising from the whole radial surface of the ulna, passing straight down into the deeper hand-layer and then radiating out to supply all digits except the prepollex.

Flexor Carpi Radialis
Figures 19, 81 to 85, 88, 91, 98

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> From the entepicondyle of the humerus and from the capsule of the elbow joint	<i>Origin</i> From the entepicondyle of the humerus and from the capsule of the elbow joint
<i>Insertion</i> Distal part of radius on flexor surface and on radial side, and on radial part of radiale	<i>Insertion</i> Entire radial border of radius, on radial side of radiale, and on radial side of wrist capsule
<i>Innervation</i> Ramus profundus of N. brachialis longus inferior	<i>Innervation</i> Ramus profundus of N. brachialis longus inferior

In both *Megalobatrachus* and *Sphenodon* this muscle takes its origin from the entepicondyle in close juxtaposition to the insertion of the M. coracobrachialis longus and from the radial part of the joint capsule. In

Megalobatrachus (Figs. 81, 82, 85), it forms a single mass which inserts on the distal end of the radius and on the radiale. In *Sphenodon* (Figs. 83, 84, 88, 98), it arises by two heads, one from the entepicondyle and the other from the entepicondyle and the joint capsule. The first and most radial of these inserts along the whole radial border of the radius, forming a broad, thin muscle which inserts along its inner edge, while the outer edge is free. The second and ulnar slip is narrower and inserts on the radiale.

As the double muscle of *Sphenodon* is obviously a more specialized condition, the flexor carpi radialis in *Eryops* (Fig. 91) was doubtless a single mass more like that of *Megalobatrachus*, but very powerful like all the flexors, as shown by the greatly developed entepicondyle. There is a conspicuous ridge on the proximal part of the entepicondyle on its lower border and just at the angle posterior to the insertion surface of the M. coracobrachialis. This is in the proper position for the origin of this muscle. There is a clearly marked facet on the distal half of the radius on the radial side which can be nothing but its radial insertion, while its most medial fibres found their insertion on the radiale as in both *Megalobatrachus* and *Sphenodon*. It was thus the chief flexor muscle of the proximal part of the radial series of elements as distinguished from the ulnar muscles occupying the greater part of the hand and lower arm.

Pronator Quadratus
Figures 94 to 98

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Entire radial side of the ulna	<i>Origin</i> Nearly the entire radial side of the ulna
<i>Insertion</i> Fibres run obliquely to the radial border of the radius, the whole flexor surface of the radiale, and the flexor surface of carpale I	<i>Insertion</i> Distal half of radius and ulnar corner of radiale
<i>Innervation</i> Ramus profundus of N. brachialis longus inferior	<i>Innervation</i> Ramus profundus of N. brachialis longus inferior

This is the deepest muscle of the lower arm. It arises from almost the entire radial border of the ulna, crosses obliquely the membrana intermuscularis connecting the ulna and radius, immediately ventral to the

ramus profundus of the N. brachialis longus inferior, which innervates it, and inserts on the ulnar border of the radius. The fibres in *Megalobatrachus* (Figs. 94, 95) are approximately parallel in their course, thus forming a quadrate muscle with an insertion about equal in extent to its origin. In *Sphenodon* (Figs. 96, 98), the fibres converge and insert on the distal half of the radius, thus forming a more triangular muscle with a strong proximodistal pull.

In *Megalobatrachus*, the distal half of this muscle continues in its more superficial fibres, as a flat, fleshy band, over the distal face of the ulna, to insert strongly on the whole flexor surface of the radiale and on carpal I. Osawa does not mention the latter insertion, but it is very clear in my dissection. This part of the muscle thus forms a powerful pronator carpi. It is not found in *Sphenodon*.

The strong development of this slip, its extreme radial insertion on both the radial elements of the carpus, to which it is limited, and the innervation from the ramus profundus suggest that this is the more distal part of that series of radial muscles which I conceive as having been originally the musculature of the prepollex of *Eryops*. That *Eryops* had a well-developed prepollex is shown in the discussion of the skeleton of the manus (page 188 and Fig. 21). The articulation of this element is so clear that it must have been a movable feature and thus must have required a musculature. The radial musculature herewith described, together with that on the extensor surface, is in the exact position demanded by such an element, and upon its disappearance the distal fibres because of their oblique position were taken over as a supinator and pronator of the hand.

The pronator quadratus was present in *Eryops*, as shown not only by its presence in both urodeles and reptiles, but also by the opposing ridges on the inner edges of radius and ulna, while the proximal position of the ulna with reference to the radius (figure 21) postulates a proximodistal direction of its oblique fibres in a line with the prepollex. Likewise, on the lower radial edge of the ulna there is a broadening of the ridge suggesting the origin of a powerful muscle band like that in *Megalobatrachus*, which is thus indicated as the "flexor prepollicis" in the restoration of *Eryops* (figure 97).

Palmaris Profundus Dorsalis

Figures 82, 86, 98

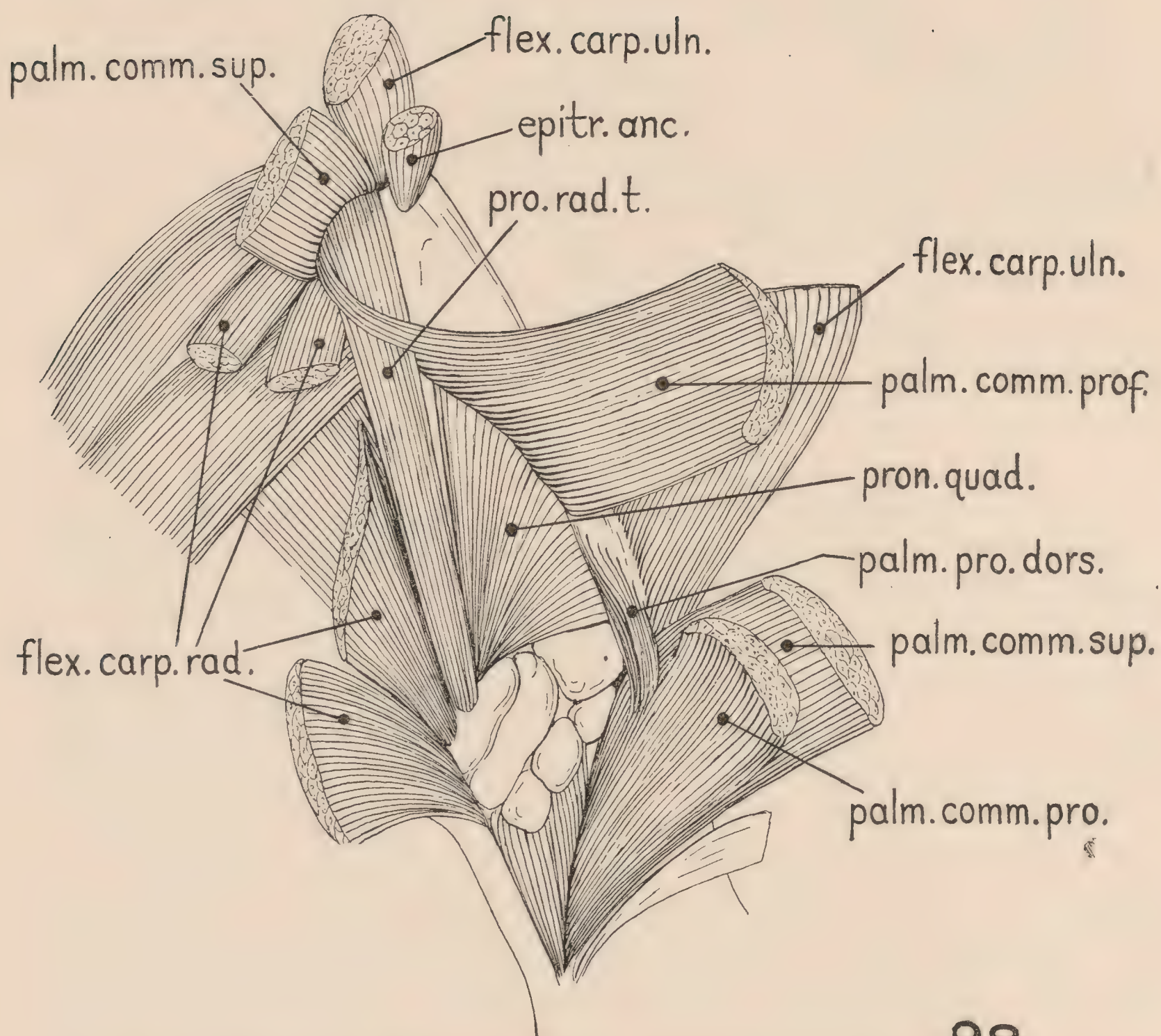
MEGALOBATRACHUS	SPHENODON
<i>Origin</i> Deeper and dorsal to the heads of M. palmaris communis profundus. Arises from nearly the whole radial angle of the ulna	<i>Origin</i> With oblique fibres from the ventral surface of the ulnar side of the distal end of the ulna
<i>Insertion</i> Dorsal side of wrist aponeurosis radial to insertion of ventral head of M. palmaris communis profundus	<i>Insertion</i> Dorsal side of palmar aponeurosis
<i>Innervation</i> Ramus profundus of N. brachialis longus inferior	<i>Innervation</i> Ramus profundus of N. brachialis longus inferior

This is a deep muscle overlying the preceding, arising like a more superficial layer of it and with oblique fibres inserting radially on the dorsal side of the aponeurosis of the M. palmaris communis superficialis, deeper than the other deep heads of that system. At first sight, it seems associated with these elements, which, as already shown (page 270), are grouped as the M. palmaris communis profundus. The innervation from the ramus profundus, however, marks it as a part of the radial system which has become connected with the palmar aponeurosis.

In *Megalobatrachus* (Figs. 82, 86), it arises from nearly the entire radial border of the ulna, and is a well-developed muscle, but in *Sphenodon* (Fig. 98), it is reduced to a mere vestige, arising from the ventral side of the distal end of the ulna and with but a slight insertion on the aponeurosis.

The relations of the whole series of forearm flexors correspond closely with those of *Amblystoma*, *Plethodon* and various reptiles described by McMurrich in his admirable paper on "The Phylogeny of the Forearm Flexors" (1903), and they may therefore be considered as typical of both amphibians and reptiles.

In *Eryops*, there is a facet on the radial face of the distal third of the ulna, which may have belonged to this muscle, though it is possible that in stegocephs it may not have separated definitely from the ventral surface of the pronator quadratus, of which it may have been the superficial portion in especial association with the "flexor prepollicis."



98

Fig. 98.—Dissection of the forearm of *Sphenodon* to show Mm. pronator quadratus, pronator radii teres, and palmaris profundus dorsalis.

Flexores Breves Sublimes

Figures 81 to 84, 89, 99, 101

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> As a series of slips in three layers from the dorsal side of the palmar aponeurosis of M. palmaris communis superficialis, where it divides into four slips for the ventral side of each finger. Figs. 101 A and B, flex. br. subl. (a), (b), (c)	<i>Origin</i> As a series of slips in three layers: (a) <i>Superficial layer</i>—from an aponeurosis formed by the conjoined proximal ends of the slips, situated in the palm of the hand, over-arching superficially the palmar aponeurosis of the M. palmaris communis superficialis and its attached muscles. Fig. 101 C, flex. br. subl. (a) (b) <i>Middle layer</i>—arising from the ventral surface of the palmar aponeurosis (of M. palmaris communis superficialis) just proximal to its subdivision into the phalangeal tendons. Fig. 101 C, flex. br. subl. (b) (c) <i>Deep layer</i>—arising from the dorsal surface of the palmar aponeurosis of M. palmaris communis superficialis. Fig. 101 C, flex. br. subl. (c)
<i>Insertion</i> All three layers of slips pass distally and insert, after uniting, on the metacarpophalangeal capsule	<i>Insertion</i> (a) <i>Superficial layer</i>—divides into five pairs of slips, one pair for each phalanx, which reunite to terminate in a trough-shaped tendon, which inserts, after traversing the basal phalanx, on the basal joint of the succeeding phalanx (b) <i>Middle layer</i>—In pairs (typically) on the metacarpophalangeal joints of digits II–IV (c) <i>Deep layer</i>—beneath the above on digits II–IV
<i>Innervation</i> Branches from loop formed by union of rami superficiales medialis and ulnaris of N. brachialis longus inferior	<i>Innervation</i> Rami superficiales medialis and ulnaris of N. brachialis longus inferior

The homology of these muscles in urodeles and reptiles has been a stumbling-block to many comparative anatomists, because of their differing relations to the aponeurosis and tendons of *M. palmaris communis superficialis* in the two groups.

Osawa and Günther have interpreted the muscle here described for *Sphenodon* as the homologue of *M. palmaris communis superficialis* in urodeles under the name of *flexor communis digitorum sublimis*, though it arises only in the hand, and call the flexor which arises from the ent-

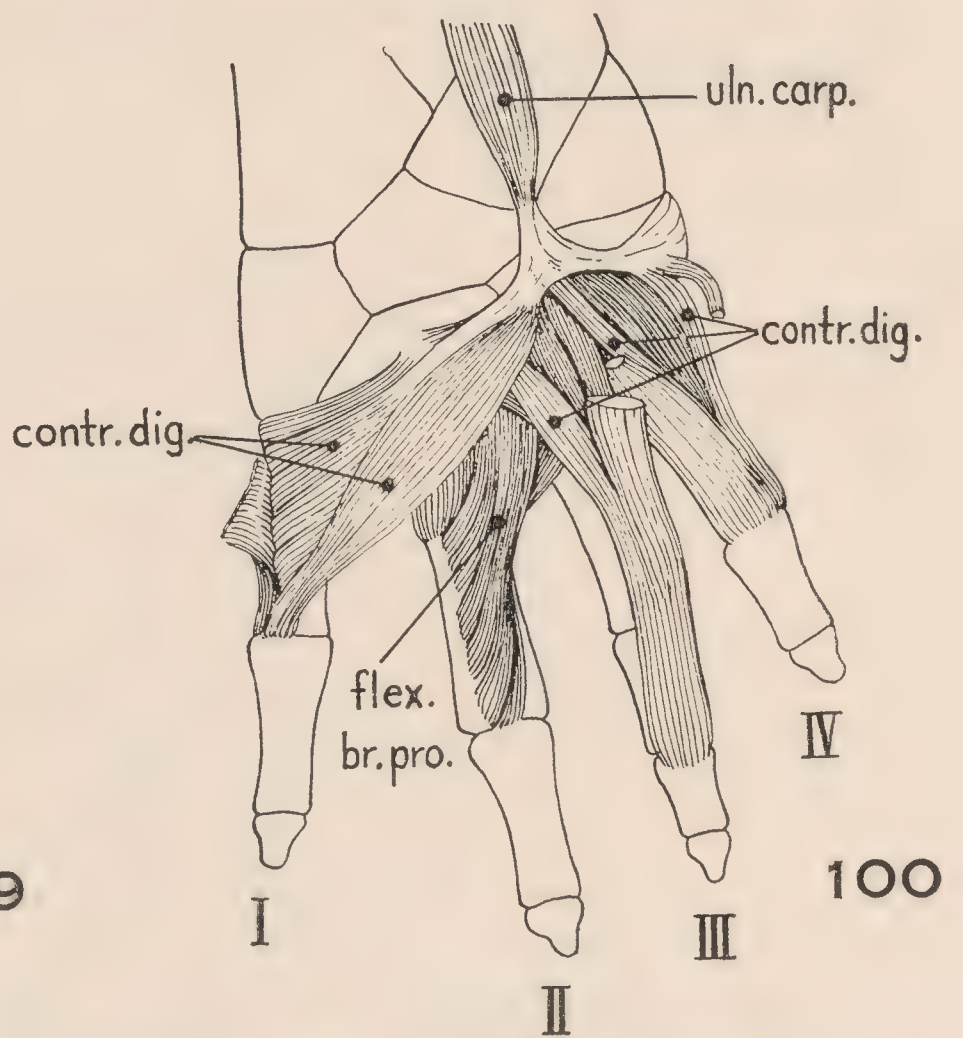
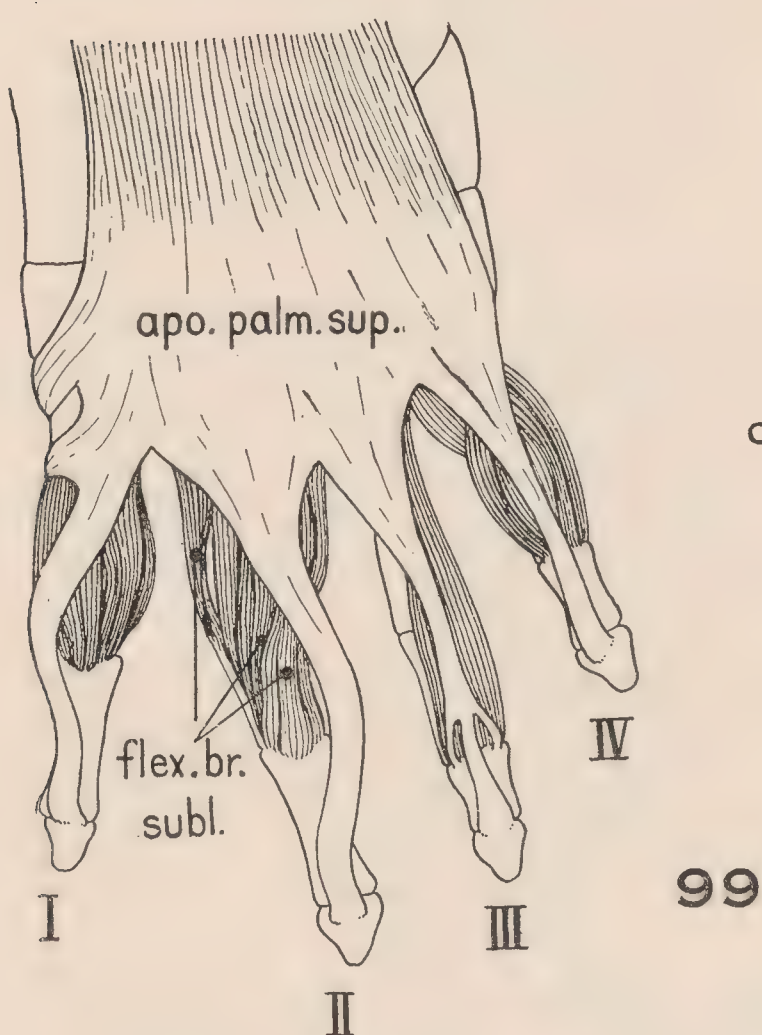


Fig. 99.—Dissection of the hand of *Megalobatrachus* to show its more superficial flexors and their attachment to the aponeurosis palmaris superficialis.

Fig. 100.—Dissection of the hand of *Megalobatrachus* to show its deep flexors and their relation to the *M. ulnocarpalis*.

epicondyle of the humerus and inserts at the terminal phalanges, the *flexor communis digitorum profundus*. (Osawa, 1898, pp. 560, 564; Günther, 1867, p. 614.)

This is because the *M. flexor brevis* (superficial layer) is situated superficially to the long flexor in reptiles (Fig. 83), while in urodeles the latter is the most superficial muscle (Figs. 81, 82). McMurrich (1903, p. 206) explains the difficulty by assuming that the superficial aponeurosis of the long flexor of urodeles has disappeared in reptiles, leaving the flexores breves exposed as the superficial layer. Ribbing, however (1907, pp. 598–599), has shown that *Emys* (flexores breves superficiales)

presents a transitional condition which clarifies the situation, and after carefully dissecting and comparing the palmar musculature in *Megalobatrachus* and *Sphenodon*, I have come to agree with the interpretation suggested by him. Figures 101 A-C in connection with the following considerations will make this clear.

In *Megalobatrachus*, as above stated, the M. palmaris communis superficialis, the long common flexor of the fingers, arises from the entepicondyle and, with its deeper heads, is the principal muscle of the ventral side of the lower arm. It is fleshy until it reaches the wrist, when it terminates in the tough connective tissue of the palmar aponeurosis. This latter feature covers the entire palmar musculature superficially, and splits into four tendons for the ventral side of the four digits. These terminate at bases of the end phalanges. The dorsal side of this aponeurosis gives rise to three layers of phalangeal muscles, shown in their most typical condition in digit II (figures 99, 101 A, B). The most distal and superficial of these muscles originates as a single slip which immediately splits into three portions, one median and two lateral, which unite at their edges distally and insert side by side on the metacarpophalangeal capsule and the base of the proximal phalanx.

The second layer likewise arises as a single muscle, proximal to the above, and likewise divides into three slips, which unite with the first set and insert immediately beneath it. The third layer arises from the dorsal side of the palmar aponeurosis, and after dividing into three slips like the other two layers, inserts in common with them.

In *Sphenodon* (Figs. 83, 84, 89), the palmaris communis of the lower arm has a similar origin and insertion to that in urodeles, as shown in the discussion of that muscle (page 267). Two of the three layers of flexores breves, however, have come to lie ventrally and superficially to it, in the following manner.

The superficial layer of flexores breves (Fig. 83) arises as a single, thin, nearly aponeurotic layer in the palm of the hand, spanning the underlying musculature, and anchored on the ulnar side by a strong connection with the pisiform, and on the radial side by a ligament binding it to the radial border of the wrist. This common origin quickly splits into five portions, one for each of the five digits. Each of these again subdivides and passes around the respective tendons of the M. palmaris communis superficialis, uniting beneath to form an arch or ring (Fig. 101 C). Each pair then terminates in a trough-shaped tendon, which passes distally beneath the palmaris tendon the distance of one phalanx to insert on the base of the succeeding phalanx. (See also Figs. 84, 89,

flex. br. subl. a.) Owing to the phalangeal formula of *Sphenodon*, this results as follows:

Digit	I,	tendon	inserts	on	base	of	phalanx	I
"	II,	"	"	"	"	"	"	II
"	III,	"	"	"	"	"	"	III
"	IV,	"	"	"	"	"	"	IV
"	V,	"	"	"	"	"	"	II

The middle layer of flexores breves arises from the superficial side of the palmar aponeurosis of M. palmaris communis superficialis, just distal to the junction of the main muscle mass with it (Figs. 84, 89, 101 C), and immediately divides into four fleshy slips (Figs. 84, 89, flex. br. subl. b.), of which the most radial passes to the radial side of phalanx II, and inserts on the proximal end of its basal phalanx; the second slip passes between metacarpalia II and III, to insert on the radial side of basal phalanx III; the third also divides and inserts on the ulnar side of basal phalanx III and the radial side of basal phalanx IV, while the fourth splits in like manner to insert on the ulnar side of basal phalanx IV and the radial side of basal phalanx V.

The deep layer of flexores breves (Fig. 101 C, flex. br. subl. c) arises from the dorsal side of the palmar aponeurosis immediately opposite to the middle layer, and divides into four slips which insert on the basal phalanges of digits II, III and IV immediately beneath and in a similar manner to the corresponding slips of the middle layer, except that there is no slip to digit V.

Thus it is evident that, in *Megalobatrachus* and *Sphenodon*, the arrangement of the layers of these muscles compare, as follows:

MEGALOBATRACHUS	SPHENODON
1. Palmar aponeurosis	
2. Superficial layer	Superficial layer
3. Middle layer	Middle layer
4.....	Palmar aponeurosis
5. Deep layer	Deep layer

In *Megalobatrachus* (Fig. 101 A, B), the palmar aponeurosis is superficial to all three muscle layers, while in *Sphenodon* (Fig. 101 C), two layers of muscles are superficial to the aponeurosis.

The most satisfactory explanation is as follows: In *Megalobatrachus* we have the more primitive condition, which in the case of terrestrial reptiles, in order to strengthen the muscular action of the toes, was followed by a gradual growth upward of the lateral muscle slips seen in figure 101 C, until their proximal portions invaded the surface of the

palmar aponeurosis, while the median portion gave way to a median tendon which formed the insertion of the lateral slips. This produced the superficial layer. A further development of the proximal ends of these slips and a further encroachment caused them to coalesce above to

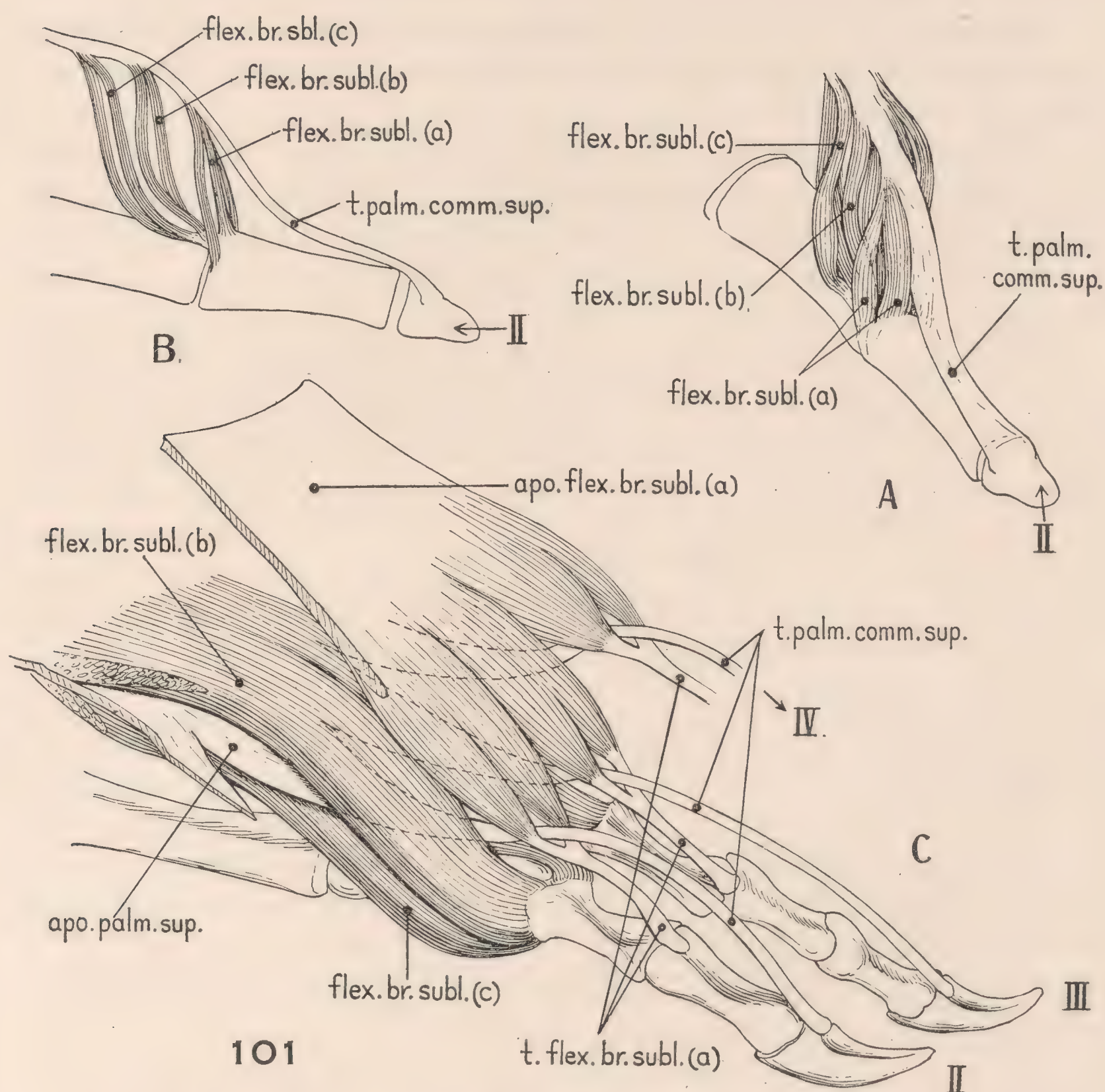


Fig. 101.—Dissection of digit II in the hand of *Megalobatrachus* (A and B), and of II, III and IV in the hand of *Sphenodon*, to show, for comparison, the relations of the digital flexors to the palmar aponeurosis. (See pages 283 to 286).

form a thin muscular sheet, which appropriated enough of the superficial connective tissue beneath the skin to form a semitendinous expanse. This finally found an attachment on the pisiform and the capsule of the wrist.

The middle layer followed the example of the superficial layer and came to lie just dorsal to it, attaching itself to the superficial surface of

the palmar aponeurosis of the palmaris communis. This layer continued to retain its old insertions on the basal phalanges, but without forming tendons, while its median slips disappeared or united with the lateral slips. The deep layer remained in its original position which corresponds in the two forms.

Ribbing (1907, pp. 598–599), as above mentioned, shows that *Emys* presents a stage in which the dorsal slips have begun to invade the ventral side of the aponeurosis.

Various reptiles carry this specialization further. In *Lacerta* and *Teius*, the superficial layer has seized hold of the ulnar part of the M. palmaris communis and has separated it from the radial part to form a continuous muscle terminating in the flexores breves without the intermediary of the pisiform.

In *Eryops* (Fig. 92), the more primitive condition naturally prevailed, as the reptilian condition is seen to be secondary, and a specialized advancement. In the restoration of the *Eryops* musculature, therefore, the M. palmaris communis superficialis is shown in its original superficial position.

Contrahentes Digitorum

Figures 94, 96, 97, 100

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> As six slips from tendon and tendinous carpal arch into which inserts M. ulnocarpalis	<i>Origin</i> As two slips arising from carpalia 2, 3, 4 and the ulnare (Adductores pollicis and digiti minimi, Osawa)
<i>Insertion</i> (a) Digit I–2 slips, one to radial side of metacarpophalangeal capsule; the other to whole radial side of first metacarpal (b) Digit II—slip to metacarpophalangeal joint (c) Digit III—slip to flexor brevis muscle mass inserting on metacarpophalangeal capsule (d) Digit IV—2 slips, one to radial side of metacarpophalangeal joint; the other to extreme ulnar side of the same joint and of metacarpus IV	<i>Insertion</i> (a) Ulnar side of metacarpophalangeal joint of digit I (b) Radial side of metacarpophalangeal joint of digit V
<i>Innervation</i> Rami superficiales medialis and ulnaris of N. brachialis longus inferior	<i>Innervation</i> (a) Ramus superficialis medialis of N. brachialis longus inferior (b) Ramus superficialis ulnaris of N. brachialis longus inferior

In *Megalobatrachus* (Figs. 94, 100), the six slips comprising these muscles are continuations of the M. ulnocarpalis through the intermediary of the deep carpal tendinous arch. The different muscle elements are so blended with this delicate arch that they appear, as Ribbing suggests (1907, pp. 624-625), to be the remnant of a former much stronger deep common flexor continuous with that muscle. In Anura this is carried a step further, where the contrahentes originate from the carpus but radiate from the same ulnar location. In reptiles (e.g., *Sphenodon*, Fig. 96), they appear to be reduced simply to the muscles known to authors as Mm. adductores pollicis and digiti minimi. This is borne out by the innervation, by the place of origin on the carpus, and by the fact that a muscle to digit I, in *Megalobatrachus*, corresponds in origin, shape, course, insertion and mechanical action with M. adductor-pollicis (auct.) in reptiles, while the slip to the ulnar border of digit IV arises from a position on the superficial side of the arch corresponding to that of the muscle just mentioned, and is in a position suggestive of a slip to the vanished digit V of urodeles. The phylogeny of the prominent oblique muscles, known as the adductors of the first and fifth digits, receives a satisfactory explanation only in this way. The slips to the three middle digits have disappeared, superseded mechanically by the increased development of the Mm. flexores breves profundi.

On the radial side of metacarpal I, the tendinous arch terminates in a broad muscular sheet partly overlapped distally by the oblique slip to the digit. This helps to strengthen the arch and with the other slip acts as a strong adductor for this digit. Its position, as in the case of the corresponding slip of the superficial palmar aponeurosis, suggests that it may have been originally the adductor of the former prepollex.

The ulnar slip to the first digit and its relation to the musculature, strongly confirms the view that this digit in urodeles is homologous with digit I of reptiles, and not digit II, as was formerly supposed by many authors, since it forms a typical pollical musculature.

The slips to digits II and III and the radial side of IV arise from the deeper side of the tendinous arch, while both of those to digit I and the slip to ulnar side of digit IV arise from its superficial side.

Since the condition in urodeles is clearly the more primitive, we may assume that it more nearly resembled the stegocephalian musculature, and hence that of *Eryops* (Fig. 97), with an adductor to the prepollex added. The theory is advanced that, as the marginal digits disappeared in the evolution of the tetrapod hand, their basic musculature was added to the outer margins of the carpus and metacarpus to form supinators and adductors, thus strengthening and perfecting the action of that organ.

Flexores Breves Profundi

Figure 100

MEGALOBATRACHUS	SPHENODON
<i>Origin</i> From the carpals of the distal row,—four small muscles	<i>Origin</i> Four muscles from metacarpals II to V, and to a certain extent from the adjacent carpalia
<i>Insertion</i> Each slip inserts on its appropriate metacarpal along its ventral face beneath the more superficial flexores breves	<i>Insertion</i> Each muscle divides, sending a radial slip to metacarpals I to IV respectively, inserting on their ulnar sides, and the other to the distal part of the metacarpal from which it arises
<i>Innervation</i> Branches from rami superficiales medialis and ulnaris of N. brachialis longus inferior	<i>Innervation</i> Rami superficiales medialis and ulnaris of N. brachialis longus inferior

Except for the Mm. interossei, these are the deepest flexors, and, as McMurrich (1903) has pointed out, are situated dorsally to the nerves above mentioned, while the more superficial flexores breves and the contrahentes digitorum are situated ventrally to them.

In the urodeles (Fig. 100), they arise from the distal carpalia and insert on the respective metacarpals, while in reptiles they are more differentiated, as is sufficiently shown in the above table.

In *Eryops*, the large size of the distal condyles of the metacarpals indicates a considerable muscular insertion. Hence we may assume that these deeper muscles, as well as the more superficial digital musculature, found their attachment there. For the origins we are justified in inferring the more primitive condition shown by urodeles, as arising from the distal carpalia.

Interossei

MEGALOBATRACHUS	SPHENODON
<i>Origin.</i> Three little muscles between the digits. They arise from the radial side of metacarpals II, III and IV	<i>Origin</i> Four tendinous bands which arise from metacarpals I, II, III and V, from the ulnar side of the first three and from the radial side of the last
<i>Insertion</i> On the ulnar side of metacarpals I, II and III	<i>Insertion</i> On the radial side of metacarpals II, III and IV, and on the ulnar side of IV
<i>Innervation</i> Branches from rami superficiales medialis and ulnaris of N. brachialis longus inferior	<i>Innervation</i> None

These deepest muscles occur generally in urodeles. In reptiles, however, they are reduced to tendinous bands. As the fleshy condition is the more primitive, we may assume for *Eryops* their presence as in *Megalobatrachus*. It is worthy of note that in *Sphenodon*, digit IV receives two insertions and gives rise to no origins.

Since the insertions are at the distal ends of the metacarpals, while the origins are more proximal, the result would be a more efficient support for digit IV, a fact that may be correlated with its greater length.

Like the Mm. flexores breves profundi, the Mm. interossei are situated dorsal to the innervation, and hence may be grouped as offshoots of the profundi series.

G. THE FLEXOR ARM MUSCLES IN GENERAL

The flexor arm muscles on the ventral side of the upper arm, which correspond to the anconæus extensor system on the dorsal side, consist of the Mm. coracoradialis proprius, coracobrachialis longus and brachialis inferior in urodeles; and Mm. coracobrachialis longus, biceps brachii and brachialis inferior in lizards. These arise like the anconæus either from the shoulder girdle or the humerus, and insert on the proximal part of the radius, or on the humerus in close connection with the ventral side of the elbow joint, as the anconæus inserts on the proximal part of the ulna on the dorsal side. Thus, as the ulna is the bone of the lower arm associated with the converging upper arm extensors, so the radius is the bone of the lower arm associated with the converging upper arm flexors.

Mm. supracoracoideus and coracobrachialis brevis should also be included, at least indirectly, with this part of the flexor system, since M. coracoradialis proprius is an offshoot of the former, and there is good reason to believe that M. biceps brachii is derived from the latter in its proximal region, as well as from M. coracobrachialis longus in its distal region, thus accounting for its double innervation (page 224). In this connection, it is worthy of note that this method of accounting phylogenetically for the doubly innervated M. biceps brachii of the flexor system in *Sphenodon*, helps to make understandable the theory advanced (page 249) regarding the origin of the apparently doubly innervated and anomalously placed muscle of the extensor system of *Megalobatrachus*, known as the M. anconæus coracoideus.

This flexor system of the upper arm, again paralleling the extensors, is continued to the lower arm by the series of flexors arising from the entepicondyle of the humerus, which is therefore the flexor condyle.

Again, as in the case of the extensors, the muscles arising from the distal part of the condyle insert on the ulna and practically the entire carpus. These are the Mm. flexor carpi ulnaris, epitrochleanconæus, ulnocarpalis, palmaris communis superficialis, and palmaris communis profundus (both heads). The M. pronator radii teres is an exception in its insertion on the radius, but since it is evident (page 270) from its innervation and origin that it is an offshoot of the M. palmaris communis profundus, it is equally clear that it belongs to the ulnar series.

Again closely paralleling the extensor side, this system is continued into the hand by the intrinsic flexor hand muscles, most of which originate from the ulnar side of the carpus and radiate into the fingers from that location.

On the contrary, and also in close parallel with the extensor condition, the lower arm muscles which arise from the proximal part of the condyle, namely, the two slips of the flexor carpi radialis, insert respectively on the radius and the radiale, and thus belong to the radial ray of the carpus, which we have seen (page 266) originally terminated in the prepollex.

Here again the arrangement of the musculature corresponds with the arrangement of the bones of the lower arm and the hand in such a way as to confirm the argument (Gregory 1915, pp. 363–364), based on the skeleton, that the present manus and carpus of tetrapods form an ulnar pyramid, which primitively arose from rays articulating from the ulnar element of the lower arm, while the prepollex was the termination of the radial element.

In the manus, the special musculature of the thumb in reptiles is exactly paralleled in its essentials in urodeles, thus confirming the view that the radial digit of urodeles is homologous with that of reptiles and is therefore actually digit I, and not digit II, as assumed by many authors, while the ulnar muscles of the lower arm, as shown on pages 266, 273 indicate a more extensive loss of primitive digital rays on that side than on the radial border of the manus where the prepollex is the only element known to have disappeared.

SECTION III. SUMMARY AND CONCLUSIONS

A. SKELETON

The Shoulder Girdle

1. In *Eryops*, the coracoidal portion of the scapulocoracoid is continued medially by a cartilaginous expansion, as shown by articulating grooves on the border of the fossil skeleton. These probably overlapped on the median line as in urodeles.

2. The clavicles of *Eryops* did not overlap on the median line as maintained by Case.

3. There was a short cartilaginous precoracoidal region like that of *Sphenodon*, extending forward beyond the clavicle.

4. The anteroventral skeleton is a freely articulating complex, in which the lateral angles of the interclavicle are embraced by the cartilaginous expansions of the coracoid dorsally, and the median ends of the clavicles ventrally, thus extending the freedom of movement of the humerus by moving the scapulocoracoid back and forth with it.

5. Contrary to Watson's view that the head of the humerus had a very limited motion in the glenoid, of a rocking character, it is shown that the strap-shaped condyle sliding forward and backward through the screw-shaped glenoid turned through an arc of about ninety degrees. This motion was extended by the free play of the clavicular-interclavicular-coracoid complex, by the rocking motion of the entire body and the play of the spine.

6. The bony portion of the *Megalobatrachus* girdle is a scapulocoracoid like that of *Eryops*.

7. The supracoracoid foramen marks the precoracoidal region and is a landmark of importance.

8. When derm bones of the girdle have disappeared in phylogeny, the underlying cartilaginous elements often become greatly expanded to compensate for the loss of the concentrated and strong dermal units, and to these their muscle attachments are transferred.

9. *Eryops* had cartilaginous ventral ribs, which probably coalesced in a sternal apparatus, as shown by the terminal articular surfaces of the bony ribs. These in turn may have articulated with a cartilaginous sternum.

10. The dermal scutes of *Eryops* overlapped the cartilaginous sternum, as the abdominal ribs of *Sphenodon* overlap its sternum, but to a greater extent.

11. The ventral segmental chondrifications, supposed by Wilder to represent the first stages of an evolving sternum, probably indicate abortive attempts to reproduce the ventral dermal armature of stegocephs.

The Limb Bones

1. The humerus of *Eryops* forms a tetrahedral prism. It closely corresponds with that of *Sphenodon*, but with much-shortened shaft.

2. It has clear evidences of the origin and insertion of muscles homologous with most of the muscles of *Sphenodon* and *Megalobatrachus* attached to it.

3. It has an ectepicondylar notch homologous with the ectepicondylar foramen of reptiles, bounded anteriorly by a projecting process for the supinator muscle, to which the name "supinator process" is here given.

4. There is no entepicondylar foramen.

5. The humerus of *Megalobatrachus* is adequately described and figured for the first time.

6. The humerus of both urodeles and reptiles is readily derived from the humerus of *Eryops*; that of *Sphenodon* by lengthening the shaft, the addition of epicondylar foramina, and the shortening and straightening of the proximal condyle; that of *Megalobatrachus* by the loss of all processes and failure of ossification in the region of the extremities, and only a slight lengthening of the shaft.

7. In addition to the points made by Gregory, Miner and Noble regarding the carpus of *Eryops*, it may be stated that the notch in the intermedium articulates with the ulnardistal angle of the radius on its distal side, as a result of arching the carpus so that the wristbones properly fit; that there is a foramen surrounded by the intermedium, ulnare, carpale 5 and the centrale (radiale). It is also suggested that the articulation of the prepollex is sufficiently important to show that it was a small jointed phalanxlike structure which may have been functional, as is later confirmed through an analysis of the lower tetrapod musculature.

8. The short metacarpals of *Eryops* are a primitive feature.

9. The phalangeal formula of lower tetrapods emphasizes the greater importance of the outside of the hand. This is correlated with the greater muscular development of the ulnar side, and the arrangement of the carpal bones to form an ulnar pyramid.

General Conclusions Regarding the Pectoral Skeleton

1. The pectoral skeleton of *Eryops* is homologous in all its essential elements with the pectoral skeleton of reptiles and urodeles, and its component parts can be homologized in detail to a great extent.

2. The pectoral skeleton of *Eryops* is more primitive than that of either urodeles or reptiles and therefore stands nearer the original tetrapod stock.

3. A musculature homologous to that of the later reptiles and urodeles is indicated for *Eryops* by the skeletal evidence as developed in the text, but of a somewhat more generalized character, and without the secondary adaptive characters evolved by many members of these groups.

4. The pectoral skeleton of *Eryops* bears evidences of attachment corresponding to the following reptilian and urodele muscles:

Trapezius	Supinator longus
Serratus	Extensor carpi radialis
	Extensor carpi profundus
Pectoralis	Extensor carpi ulnaris
Supracoracoideus	Extensor digitorum longus
Coracobrachialis longus	Dorsometacarpales
Brachialis inferior	
	Palmaris communis longus
Deltoides clavicularis	Palmaris communis profundus
Deltoides scapularis	Flexor carpi ulnaris
Scapulohumeralis	Epitrochleoanconæus
Latissimus dorsi	Small flexors of hand
Anconæus lateralis	
Anconæus medialis	
Anconæus scapularis	
Anconæus coracoideus	

Other muscles, as shown in the following section, are inferred from necessary relations to neighboring muscles, and by their presence in both the lines of reptilian and urodele descent.

B. MUSCULATURE

1. The attempt to restore the musculature of *Eryops* from the evidence of detailed muscle homologies between two lines descended

from the stegocephs, namely, the urodeles and reptiles, as exemplified by *Megalobatrachus* and *Sphenodon*, has resulted in a complete confirmation of the evidence from the skeleton, and the addition of muscle elements not indicated directly by the bones, but inferred by their occurrence in both modern types and by the necessary relations to other muscles.

2. It would be difficult to summarize the specific conclusions regarding these muscle homologies and their application to *Eryops*, in this part of the paper, without defeating its purpose as a summary. Special summaries of the homologies are given in the tables preceding the treatment of the individual muscles, while their applications to *Eryops* are given at the close of each muscle discussion.

3. From a reëxamination of the muscle homologies, and from the restoration of the musculature of *Eryops*, several new points have been brought to light, and additional evidence has been secured confirming or modifying the conclusions of other investigators. Some of these are outlined in the following paragraphs.

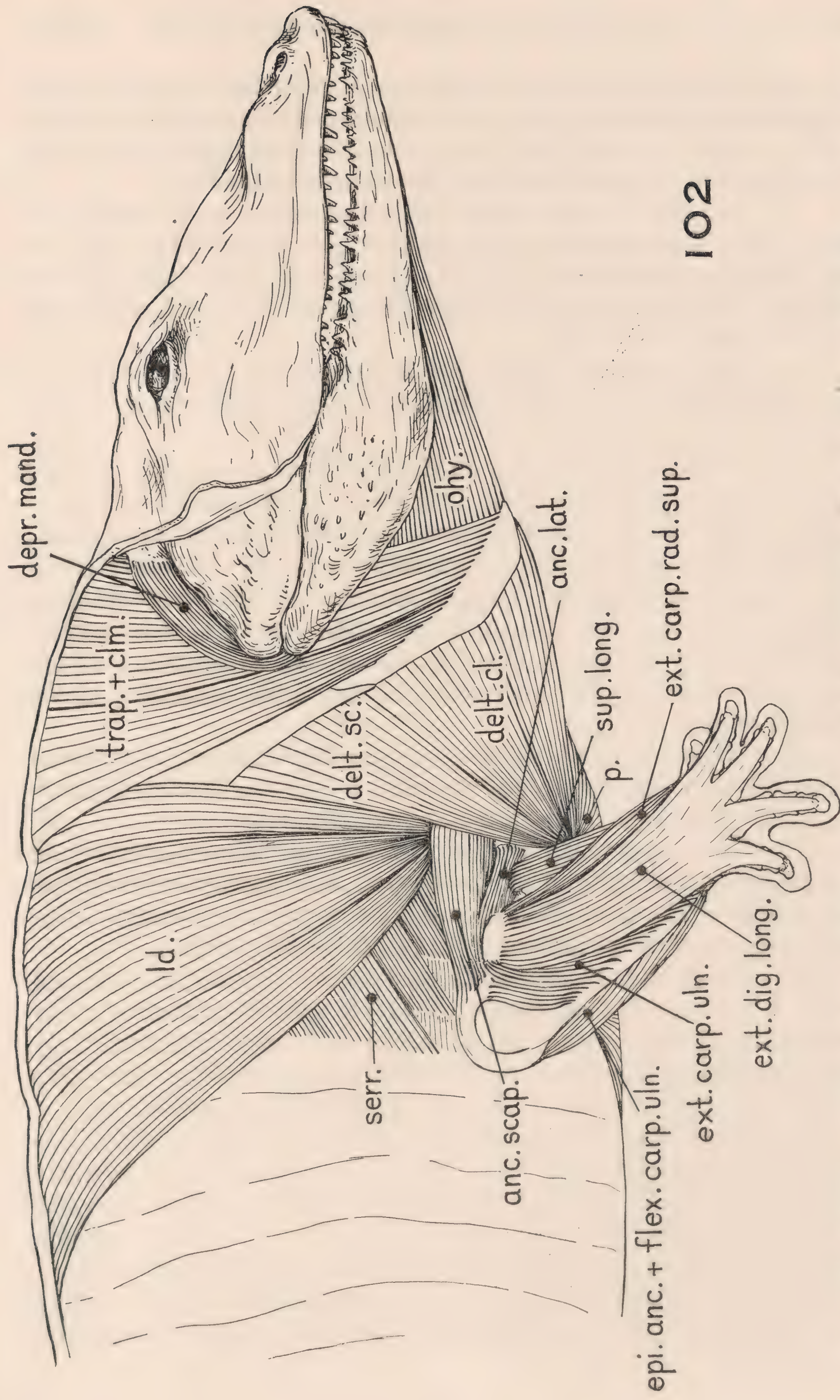
4. The visceral innervation of the M. sternocleidomastoideus is explained by interpreting this muscle as originally derived from a vanished sixth gill arch like that of primitive sharks and ganoids, which became secondarily attached to the anterior border of the shoulder girdle as its advance crowded out the sixth gill arch.

5. The levator scapulæ of *Megalobatrachus* represents an intermediate condition between the visceraally innervated levator scapulæ of fishes and the somatically innervated muscle of the same name in reptiles.

6. The serratus profundus of *Megalobatrachus* originates from two ribs instead of one, as stated by Osawa. These divide into five slips arranged in two layers homologous with the superficial and deep layers of serratus profundus of *Sphenodon*.

7. The omohyoideus and sternohyoideus in *Megalobatrachus* are homologous with the ventral system in *Sphenodon*, formed by the sternocoracoidei, costosternocoracoideus and episternohyoideus. They are anterior continuations of the rectus abdominis musculature. In *Sphenodon*, the lateral slips brace the ligamentum sternoscapulare internum anteriorly and posteriorly as the omohyoideus and costosternocoracoideus muscles.

8. The supracoracoideus muscle is not genetically connected with the pectoralis system, or with the coracobrachialis, as Romer suggests, but forms a separate anterior muscle mass, as shown by its innervation, and is secondarily fused with the pectoralis along the adjacent edges.



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Fig. 102.—Inferred restoration of the superficial musculature of the pectoral limb and girdle of *Eryops megacephalus*. Lateral view.

9 The biceps brachii of reptiles was originated by elements belonging to the coracobrachialis longus and brevis respectively, in fusion with a portion of the anterior membrana intermuscularis in the region of the shoulder joint and fibres from M. brachialis inferior.

10. The coracoradialis proprius was evolved in amphibians by the reduction of the primitive biceps brachii fibres, while a deeper layer of the supracoracoideus became attached proximally to the region of the membrana intermuscularis, on which the biceps fibres were inserted, and replaced them functionally.

11. The conditions in the *Eryops* humerus would lead equally to the evolution of either a biceps brachii or a coracoradialis proprius muscle system.

12. The muscles inserting on the caputhumeri form a fan-shaped series consisting of three systems, identified by their position and innervation. They are (a) a dorsal system with an intrazonal innervation, consisting of the latissimus dorsi, deltoides scapularis, deltoides clavicularis, scapulohumerales anterior and posterior and subcoracoscapularis muscles; (b) an anteromedian system with interzonal innervation, consisting of the supracoracoideus and coracoradialis proprius muscles; and (c) a ventral system with pectoral innervation, consisting of the pectoral muscle.

13. It is more reasonable to regard the scapulohumeralis posterior as an offshoot of the scapulohumeralis anterior than, as Romer suggests, as intimately connected with the subcoracoscapularis.

14. The anconæus muscle is divided naturally into an anterior and a posterior set consisting of two heads each, indicated by the primitive dorsal ridge of the *Eryops* humerus and the proximal separation of the two sets by the typical insertion of the latissimus dorsi muscle.

15. The tendinous origin of the anconæus scapularis on the lateral surface of the scapula in *Sphenodon*, does not mark the posterior border of the bony scapula as, Romer claims, but the tendon has shifted anteriorly from the primitive posterior position, carrying with it the connective tissue elements that form the ligamentum scapulohumerale laterale.

16. It is doubtful whether the anconæus coracoideus of *Megalobatrachus* is homologous with the anconæus coracoideus of *Sphenodon*. The former is apparently related to the M. coracobrachialis longus, and has become welded with the anconæus mass distally; the latter is a purely anconæal muscle attached proximally to a connective tissue ligament.

17. The humeroradialis of *Sphenodon* is explained as the result of the fusion of supinator longus elements with deltoid elements on opposite

sides of the supinator process, and the membrana intermuscularis. When the process receded to form the supinator crest, these elements were left attached to each other.

18. The supinator process of *Eryops* was the area of origin for the supinator longus muscle.

19. The distal part of the ligamentum intermusculare in *Megalobatrachus* is homologous with that part of the supinator crest in *Sphenodon* which is external to the ectepicondylar foramen, and with the supinator process of *Eryops*.

20. The insertion of the extensor carpi ulnaris in reptiles is associated with the fifth digit. In urodeles, it is directed toward the vanished fifth digit. Its position also indicates the original existence of a sixth digit.

21. The arrangement of the extensor digitorum longus in *Megalobatrachus* is more primitive than that in *Sphenodon*. The proximal muscle mass is homologous in both types. The extensor digitorum communis brevis plus the distal tendinous slips of extensor digitorum longus of *Megalobatrachus* are together homologous to the extensor digitorum communis brevis with its distal slips as they are seen in *Sphenodon*. It is inferred that in *Eryops* the condition was more like that in *Sphenodon*.

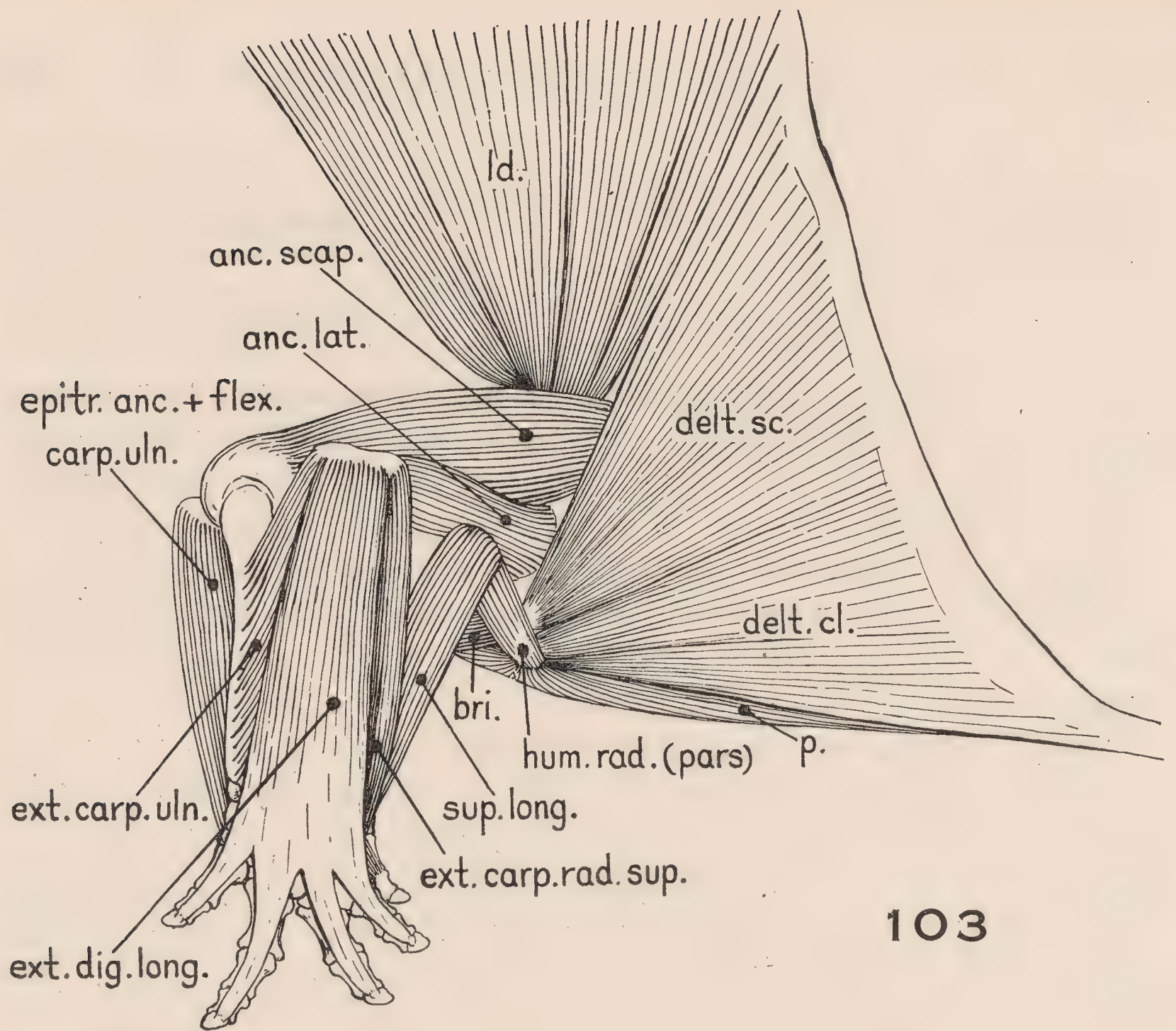
22. The extensor digitorum communis brevis arises from the ulnare and the intermedium alone, and not from the radiale and carpalia, as stated by Osawa, and thus corresponds with the condition in *Sphenodon*. There are five slips instead of four, as also stated by Osawa.

23. The muscle arrangement on the extensor side of the lower arm and hand corresponds with the arrangement of the bones in such a way as to confirm the theory of an ulnar pyramid. The muscles of the hand of reptiles and urodeles are an ulnar complex, while the radial muscles of the lower arm converge from the supinator crest to the radius and radiale and are the survival of a prepollical musculature.

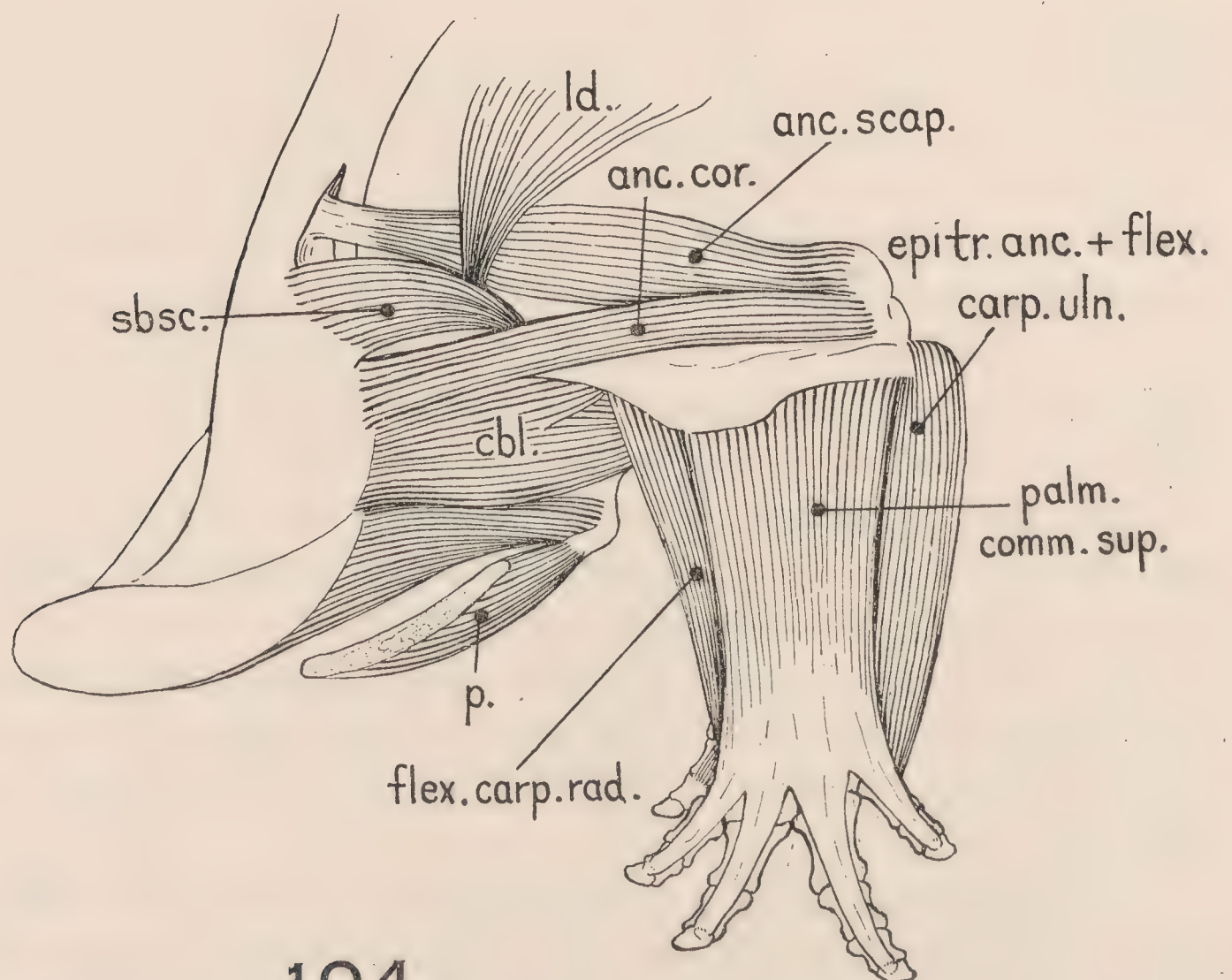
24. As *Eryops* had a prepollex, it is inferred that the radial musculature was directed to its base, and was taken over by the radial border of the lower arm and hand in later forms.

25. The muscle arrangement on the flexor side of the lower arm and hand also confirms the above view, as it is parallel to the arrangement of the extensor muscles, and also indicates the presence of a former prepollex.

26. The relations of the flexor carpi ulnaris and epitrochleoanconæus confirm the view indicated by the corresponding extensor muscles that there were originally a fifth and sixth digit on the ancestral tetrapod hand.



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Fig. 103.—Inferred restoration of the superficial musculature of the pectoral limb and girdle of *Eryops*. Anterior view.

Fig. 104. Same. Posterior view.

27. The relations of the ulnocarpalis to the contrahentes digitorum in *Megalobatrachus* are demonstrated by dissection, and are shown to be rather in harmony with the observations of Ribbing than with those of McMurrich, Wilder and Osawa. The ulnocarpalis inserts by a tendon into a tendinous bridge, from which in turn arise the six slips of the contrahentes digitorum, which thus form a continuous series with it.

28. A portion of the pronator quadratus is differentiated as a pronator carpi in *Megalobatrachus*. This muscle has not been recorded before and is a clear indication of a former prepollex. It is therefore inferred for *Eryops* as a *M. flexor prepollicis*.

29. The palmar aponeurosis of the palmaris communis superficialis is situated superficially in *Megalobatrachus*, with three layers of flexores breves sublimes arising from its dorsal surface. In *Sphenodon*, two of these layers are superficial to the palmar aponeurosis, while only one layer arises from its dorsal surface. This puzzling difference is explained by McMurrich by assuming that the superficial aponeurosis has disappeared in reptiles, exposing the first two layers of breves lying on a subsidiary aponeurosis. Ribbing suggests that the condition in reptiles results from an upgrowth of the proximal ends of these slips to lie superficially. The present investigation confirms the suggestion of Ribbing, since the analysis of the muscle shows its greater reasonableness. This is discussed in detail on pages 281 to 286 of the present paper.

30. The outer slips of the contrahentes digitorum of *Megalobatrachus* are homologous with *Mm. adductores pollicis* and *digiti minimi* of *Sphenodon*. In the case of the former slip, the homology greatly strengthens the view that the radial digit of urodeles is homologous with the pollex of reptiles.

31. The theory is advanced that, as the marginal digits of the primitive tetrapod hand disappeared in the evolution toward that of modern types, their basic musculature was added to the outer margin of the carpus and metacarpus to form supinators and adductors, thus strengthening and perfecting that organ.

32. The large size of the distal metacarpal condyles of *Eryops* indicates a well-developed carpal and metacarpal musculature in that form.

33. The general conclusions regarding the extensor and flexor arm muscles as a whole are given on pp. 265 to 267, and on pp. 289 to 291.

34. It is evident that the essential musculature of modern reptiles and urodeles had already differentiated in *Eryops*, and hence within the group Stegocephalia, but correlated with more primitive skeletal features.

Hence the homologies here given for the combined amphibian-reptile stems are a key to the fundamental tetrapod musculature, and may be taken as a starting point for interpreting that of higher forms.

C. A CLASSIFICATION OF LOWER TETRAPOD MUSCULATURE

The muscles are most naturally classified according to the chief criteria by means of which they were homologized, as follows:

Torsozonal Musculature

(Muscles from body to shoulder girdle)

Anterodorsal Series

(Typically wholly or partly innervated by visceral nerves and anterior spinal somatic nerves)

¹Sternocleidomastoideus

Trapezius

¹Levator scapulæ

Dorsomedial Series

(Innervated by spinal nerves, muscles typically segmental, inserting principally on inner side of suprascapula)

¹Serratus superficialis

¹Serratus profundus

Ventral Series

(Segmentally innervated, typically with inscriptiones tendineæ, derived from ventral longitudinal musculature)

¹Omohyoideus

¹Sternohyoideus (urodeles)

Sternocoracoidei (reptiles)

Costosternocoracoideus (reptiles)

¹Episternohyoideus (reptiles)

¹Rectus abdominis

Zonocaputhumeri Musculature

(Muscles typically from shoulder girdle or body fascia—perhaps originally dermal scutes—to head of humerus)

Dorsal Series

(Innervated by axillary and related nerves)

¹Deltoides clavicularis (reptiles)

Procoracohumeralis (urodeles)

¹Deltoides scapularis (Dorsalis scapulæ)

¹Scapulohumeralis anterior

Scapulohumeralis posterior

¹Latissimus dorsi

¹Subcoracoscapularis

Anteromedian Series

(Innervated by supracoracoideus nerve)

¹Inferred for *Eryops*.

¹Supracoracoideus

¹Coracoradialis proprius (amphibians)

Ventral Series

(Innervated by pectoral nerve)

¹Pectoralis

Humeroextensor Musculature

(Extensor muscles lying on the upper arm, innervated by N. brachialis longus superior)

¹Anconæus

¹Humeroradialis (*Sphenodon*) (also axillary innervation)

Humeroflexor Musculature

(Flexor muscles on the ventral side of the upper arm, innervated by N. brachialis longus inferior)

¹Coracobrachialis brevis

¹Coracobrachialis longus

¹Biceps brachii (reptiles)

¹Brachialis inferior

Ulnoextensor Musculature

(Extensor muscles of the lower arm and hand innervated largely by ulnar branches of N. brachialis longus superior)

¹Extensor carpi ulnaris

¹Extensor digitorum longus

¹Supinator manus

¹Extensor digitorum communis brevis

¹Dorsometacarpales

Radioextensor Musculature

(Extensor muscles of the lower arm and radial border of carpus innervated by radial branch of N. brachialis longus superior)

¹Supinator longus

¹Extensor carpi radialis superficialis

¹Extensor carpi radialis profundus

Ulnoflexor Musculature

(Flexor muscles of lower arm and hand innervated largely by ulnar—superficial—branches of N. brachialis longus inferior)

¹Epitrochleoanconæus

¹Flexor carpi ulnaris

¹Palmaris communis superficialis

¹Palmaris communis profundus

¹Pronator radii teres

¹Ulnocarpalis

¹Inferred for *Eryops*.

¹Palmaris profundus dorsalis

¹Flexores breves sublimes

¹Contraahentes digitorum

Radioflexor Musculature

(Flexor muscles of the lower arm, radial border of carpus and deeper part of hand, innervated by radial—deep—branch of N. brachialis longus inferior)

¹Flexor carpi radialis

¹Pronator quadratus

¹Flexores breves profundi

¹Interossei (Intermetacarpales)

¹Inferred for *Eryops*.

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LIST OF ABBREVIATIONS

ABD. R.	abdominal ribs
ABD. S.	abdominal scutes
ACR	acromion
anc	M. anconæus
anc. cor.	M. anconæus coracoideus
anc. lat.	M. anconæus lateralis
anc. med.	M. anconæus medialis
anc. qu.	M. anconæus quartus
anc. scap.	M. anconæus scapularis
apo. flex. br. subl. (a)	aponeurosis M. flexoris brevis sublimis (superficial layer)
apo. palm. sup.	aponeurosis M. palmaris communis superficialis
bi	M. biceps brachii
bi ¹	M. biceps brachii (proximal belly)
bi ¹¹	M. biceps brachii (distal belly)
BR ¹ , BR ²	first and second branchial arches
bri	M. brachialis inferior
c	centrale
c ₁ , c ₂ , c ₃ , c ₄ , c ₅	carpalia 1, 2, 3, 4, 5.
CAP. HUM.	caput humeri
caps. j.	capsule of the shoulder joint
cbb	M. coracobrachialis brevis
cbl	M. coracobrachialis longus
CL	clavicle
clm	M. cleidomastoideus
contr. dig.	MM. contrahentes digitorum
COR	coracoid
COR. CART.	coracoid cartilage
cor. rad. prop.	M. coracoradialis proprius
cost. cor.	M. costocoracoideus
CRD	deltoid crest
CRDP	deltopectoral crest
CRP	pectoral crest
costc	M. costosternocoracoideus
CTH	cleithrum
del or delt. cl.	M. deltoides clavicularis
delt. sc. or delt. scap.	M. deltoides scapularis
depr. mand.	M. depressor mandibuli
DERM. SC.	dermal scutes
dorso. met.	MM. dorsometacarpales
D. PR.	deltoid process
dsc.	M. dorsalis scapulæ
ECTC	ectepicondyle
ECT. N.	ectepicondylar notch
ENTC	entepicondyle
episthy	M. episternohyoideus

epitr. anc.	M. epitrochleoanconæus
ext. carp. rad.	M. extensor carpi radialis
ext. carp. rad. prof.	M. extensor carpi radialis profundus
ext. carp. rad. sup.	M. extensor carpi radialis superficialis
ext. carp. uln.	M. extensor carpi ulnaris
ext. dig. comm. br.	M. extensor digitorum communis brevis
ext. dig. long.	M. extensor digitorum longus
ext. dig. quarti	M. extensor digiti quarti
FECT	ectepicondylar foramen
FENT	entepicondylar foramen
FGL	glenoid foramen
flex. br. pro.	Mm. flexores breves profundi
flex. br. subl.	MM. flexores breves sublimes
flex. br. subl. (a)	MM. flexores breves sublimes (superficial layer)
flex. br. subl. (b)	MM. flexores breves sublimes (middle layer)
flex. br. subl. (c)	MM. flexores breves sublimes (deep layer)
flex. carp. rad.	M. flexor carpi radialis
flex. carp. uln.	M. flexor carpi ulnaris
flex. prepoll.	M. flexor prepollicis of <i>Eryops</i>
FSGL	supraglenoid foramen
FSPC	supracoracoid foramen
GLEN	glenoid cavity
HUM	humerus
HUMC	condyle of humerus
hum. rad.	M. humeroradialis
HY	hyoid arch
i	intermedium
ic	MM. intercostales
ICL	interclavicle
ld	M. latissimus dorsi
LD. PR.	processus latissimi dorsi
lev. scap.	M. levator scapulæ
lev. scap. inf.	M. levator scapulæ inferior
lev. scap. sup.	M. levator scapulæ superior
lig. sch.	ligamentum scapulohumeralis
lig. stsc.	ligamentum sternoscapulare internum
m_1, m_2, m_3	medialia 1, 2, 3
mem	membrane
mem. st.-est.	membrana sternoepisternalis
$mtc_1, mtc_2, mtc_3, mtc_4$	metacarpalia 1, 2, 3, 4
N. brach. long. sup.	Nervus brachialis longus superior
N. dors. scap.	Nervus dorsalis scapulæ
N. procor. hum.	Nervus procoracohumeralis
N. spc.	Nervus supracoracoideus
ohy	M. omohyoideus
ohy ¹ .	M. omohyoideus (lateral slip)
ohy ¹¹ .	M. omohyoideus (medial slip)
p. int.	M. pectoralis interclavicularis

p	M. pectoralis
p. abd.	M. pectoralis abdominalis
palm. comm. prof.	M. palmaris communis profundus
palm. comm. prof. ¹	M. palmaris communis profundus (dorsal head)
palm. comm. prof. ¹¹	M. palmaris communis profundus (ventral head)
palm. comm. sup.	M. palmaris communis superficialis
palm. prof. dors.	M. palmaris profundus dorsalis
p. cl.	M. pectoralis clavicularis
PCOR	precoracoid
p. est.	M. pectoralis episternalis
<i>Pm</i>	postminimus
<i>Pp</i>	prepollex
PROCOR	procoracoid
procor. hum.	M. procoracohumeralis
pron. quad.	M. pronator quadratus
pro. rad. t. or p. r. teres	M. pronator radii teres
p. st.	M. pectoralis sternalis
<i>r</i>	<i>radiale</i>
R ₂ , R ₃ , R ₄ , R ₅ , R ₆	second, third, fourth, fifth and sixth ribs
RA	radius
r. abd. or rect. abd.	M. rectus abdominalis
RADC	condyle of radius
rad. sup.	M. radialis superficialis
sbesc	M. subcoracoscapularis
sbse	M. subscapularis
SC	scapula
SCCOR	scapulocoracoid
sch	M. scapulohumeralis
scha	M. scapulohumeralis anterior
schp	M. scapulohumeralis posterior
serr	serratus
serr. pro.	M. serratus profundus
serr. pro ¹ .	M. serratus profundus (superficial layer)
serr. pro ¹¹ .	M. serratus profundus (deeper layer)
serr. sup.	M. serratus superficialis
spc	M. supracoracoideus
SPG. B.	supraglenoid buttress
ST	sternum
st. cor.	MM. sternocoracoidei
stc. prof.	M. sternocoracoideus profundus
stc. sup.	M. sternocoracoideus superficialis
sthy	M. sternohyoideus
ST. R.	sternal ribs
SUP. CR.	supinator crest
sup. long.	M. supinator longus
sup. man.	M. supinator manus
SUP. PR. or SUP. PROC.	supinator process
SUPSC	suprascapula

t. bi. or ten. bi.	tendon of M. biceps
t. cor. rad. prop.	tendon of M. coracoradialis proprius
td ₁ , td ₂ , td ₃ , td ₄ , td ₅	first, second, third, fourth and fifth inscriptiones tendineæ of M. sternohyoideus
t. flex. br. subl. (a)	tendons of MM. flexores breves sublimes (super- ficial layer)
t. palm. comm. sup.	tendon of M. palmaris communis superficialis
trap	M. trapezius
<i>u</i>	ulnare
UL	ulna
uln. carp.	M. ulnocarpalis

Article VIII.—THE AFFINITIES OF THE FISH *LYCOPTERA*
*MIDDENDORFFI*¹

BY T. D. A. COCKERELL

Plate III; Text Figure 1

Among the interesting fossils obtained by the Third Asiatic Expedition of The American Museum of Natural History in 1922 were numerous fishes from the Ondai Sair formation of Mongolia, ascribed to the Lower Cretaceous. These appear on examination to be old and young of a single species, *Lycoptera middendorffi*, described by Johannes Müller in 1848 from shales supposed to be of Jurassic age, occurring in the Transbaikal region of Siberia. The problem of stratigraphy and correlation has been discussed as fully as circumstances permit in another paper, and it remains only to give a fuller account of the fish remains, which are of quite unusual interest.

Lycoptera is referred by Doctor A. S. Woodward to the family Leptolepidæ, of which he writes:²

The Leptolepidæ differ from the two preceding families [Pholidophoridæ and Oligopleuridæ] in the absence of fulcra on the fins [whereby they agree with all living Isospondylous fishes], and are remarkable as being the earliest family in which intermuscular bones occur. These elements, forming so conspicuous a feature among modern fishes, appear to be arranged here only in a single series above the vertebral column in the abdominal region; though there may perhaps be traces of them sometimes also in the lower half of the caudal region. The vertebral centra of *Leptolepis* itself exhibit interesting gradations in the degree of development according to the geological age of the species, these centra never being more than delicate constricted rings or cylinders in the Upper Lias, and always strengthened by secondary peripheral calcifications in the Oxfordian [Middle Jurassic] and upwards. In *Thrissops*, which ranges as far at least as the Lower Cretaceous, the vertebral centra are still more robust. These fishes, it will be noticed, approach very closely the Clupeidæ, among which they are sometimes included; but they are distinguished by the meeting of the parietal bones in the median line, by the non-fusion of the hæmal spines at the base of the tail, and by the presence of a thin film of ganoine on the scales. [Remarks in brackets are mine.]

Jordan and Branner³ say of the Leptolepidæ:

This family stands almost intermediate between the Ganoids and the Isospondyli. It has the general fin arrangement of the latter, but the scales are more or less diamond-shaped and ganoid on their exposed parts, and the last vertebræ are more or less turned upward, although the tail is usually or always forked. The orbital plates cover the cheek as in the Elopidae, but there is no gular plate, so far as known.

¹Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 39.

²1895, 'Catalogue of Fossil Fishes in the British Museum (Natural History),' III, p. xxi.

³1908, Smithsonian Miscellaneous Collections, LII, Part 1, p. 13.

However, a gular plate is clearly shown in Reis's figure of *Lycoptera middendorffi*.

Boulenger¹ separates the Leptolepidæ from other malacopterygian families only by the perforation of the vertebral centra, at least so far as his table shows. He recognizes that the coating of the scales with ganoin is not a family character.

We may readily gather from all this that the Leptolepidæ, beginning in the Upper Lias, represent the line of development which first points distinctly to the modern dominant isospondylous and related fishes. It is a group which therefore deserves minute analysis to determine what characters were evolving and in what manner. Gregory² has recently remarked: "The Jurassic Leptolepidæ are the earliest known true teleosts, with their cycloid scales, vertebral centra nearly complete, no fin fulcra, intermuscular bones present, and head and jaws remarkably like those of primitive Clupeidæ. The homocercal tail sometimes develops hypural bones of primitive teleost type." He here refers to Woodward's figure of tail of *Leptolepis dubius*.

An analysis of the above statements and of the known characters of the fishes serves only to bring out more clearly the relationship to existing families. The supposed family character of more or less ganoid scales breaks down entirely, as Gregory has indicated. As regards the vertebral centra, in some forms at least they appear to be well ossified, and *Lycoptera* during its lifetime goes through about the same stages described by Woodward as existing in successive species of *Leptolepis*. The distinct elevation of the end of the vertebral column corresponds to the condition found in the young of *Salmo* and other fishes.

I am particularly fortunate in being able to present some enlarged figures of the scales of *Leptolepis* and *Thrissops*, photographed by Mr. Herring under the direction of Doctor A. S. Woodward at the British Museum. The type of *Leptolepis* is *L. coryphænoides* (Bronn)³ from the Upper Lias. It may be that *L. dubius* (Blainville) from the Lithographic Stone of Bavaria is not strictly congeneric, in which case *Ascalabos* Munster may be available in a subgeneric sense. A photograph of the scales of *L. dubius* (which may possibly differ somewhat from those of the type of the genus and family) shows the following characters: scales cycloid, broader than long, apex very broadly rounded, base truncate, laterobasal angles obtuse; nucleus central; circuli fine and distinct,

¹1904, 'Cambridge Natural History,' VII, p. 544.

²1923, Bull. Amer. Mus. Nat. Hist., XLVIII, p. 241.

³*Cyprinus coryphænoides* Bronn, 1830; *Leptolepis bronni* Agassiz, 1832.

concentric; no radii. The laterobasal circuli cut the more central ones somewhat as indicated in Geinitz's figure of *Kymatolepis*, but about half-way between nucleus and margin. A distinct ridge on each side passes from the region of the nucleus to the laterobasal corner.

Now it is singular that the features of this scale, even to the interference of the circuli laterally and the indication of ridges from the nucleus to the laterobasal corners, are very nearly those of the living *Caranx hippos* (Linnæus), or *Carangus hippos* as Jordan has it. The ridges, however, are just as well seen in certain salmonoid scales, such as *Leucichthys nigripinnis* (Gill). The fish *Leptolepis dubius* is of course quite distinct from the Salmonidæ, and still more so from the Carangidæ, but I believe that the scale-structure may be regarded as prophetic. That is to say, the scale type of the modern fishes was acquired earlier than many of the other structures, and hence when found in a fossil may be used to indicate the line of development initiated by the latter. If this generalization is valid, it affords us a very important clue to the evolution of fishes. In the case of *Thrissops*, I am fortunate in having a photograph of the scales of the type species, *T. formosus* Agassiz, from the Lithographic Stone of Bavaria. The scales are extremely broad and very different from those of *Leptolepis*. They may be described as follows: scales transverse, very much broader than long; apical margin simple, broadly rounded or slightly angular; some distance below the margin, but well above the nucleus, is usually a more or less irregular or wavy band, interpreted as an annulus; occasional feeble rudiments of apical radii, but distinct basal radii of the type seen in *Ichthyodectes*; circuli extremely fine, concentric.

These scales much resemble those of the Cretaceous *Hypsodon*, lacking, however, the prominent tuberculation of the apical area. There is a superficial, but probably not significant, resemblance to the scales of the modern Hemirhamphidæ and Exocoetidæ.

Coming now to *Lycoptera middendorffi*, we find still another quite diverse type of scale (Fig. 1). The scales are minute, about 1.2 mm. across, cycloid, transversely broad oval, without corners; nucleus central; circuli fine and concentric; apical and basal radii, the basal (about 14) extending up the sides nearly to meet the apical; apical radii about 13 but weaker and shorter, irregular. In some scales the radii are less developed or evanescent.

This scale is practically identical with that of the European minnow, *Phoxinus phoxinus*. I am unable to point out any difference which could be called generic. *Lycoptera* has so much the aspect of a

cyprinid that Egerton long ago proposed to place it in the cyprinid genus *Aspius*. It is a freshwater fish, and in it I think we must see the ancestor of the Cyprinidæ and their allies.

That it is not a cyprinid is shown by the following characters.

1.—Teeth are present on the premaxilla, maxilla, and dentary, though extremely small. I could not demonstrate these teeth in my material and for a time believed them absent, but in one specimen I was able to see small sockets, and a specimen from the original (Siberian) lot in the British Museum clearly shows the teeth. Through the kindness of Doctor A. S. Woodward, I am able to present an enlarged figure of this specimen.

2.—As shown by Reis, there is a gular plate resembling that of *Amia*.

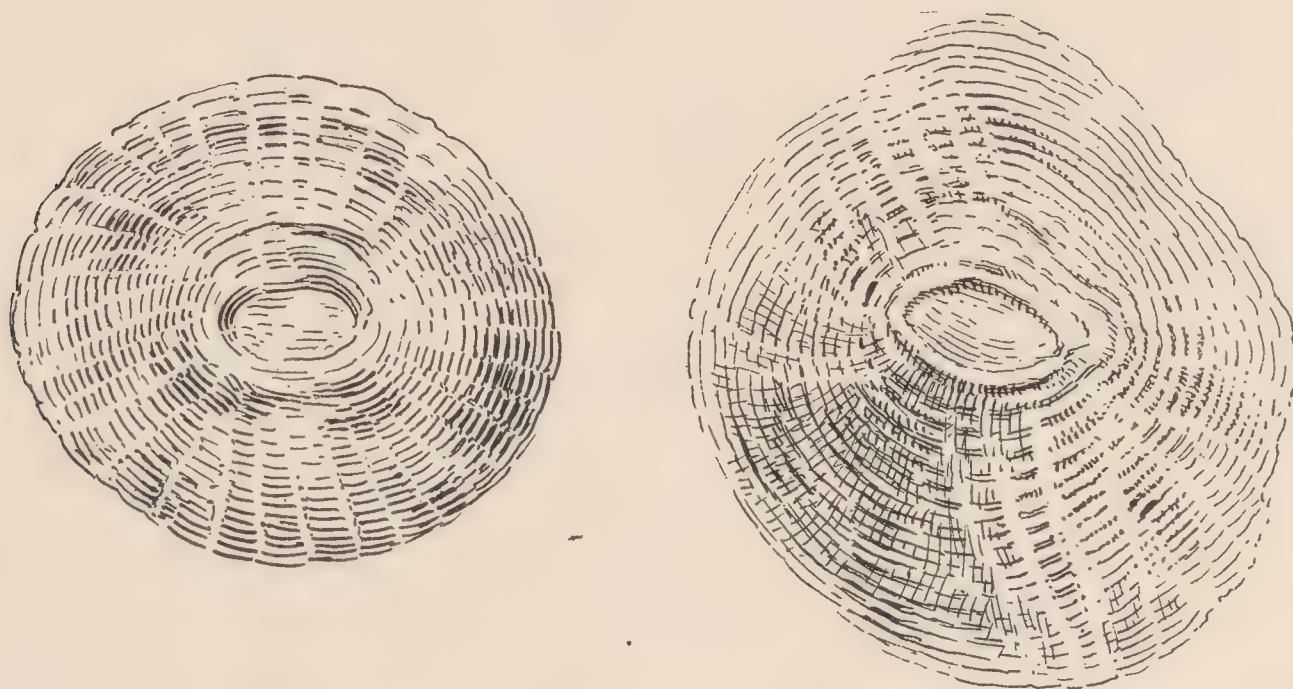


Fig. 1. Two scales of *Lycoptera* from the Ondai Sair shales, showing their general character.

3.—The end of the vertebral column turns upward, though the caudal fin is bifurcated and entirely like that of a cyprinid in appearance.

4.—The anterior vertebræ are not modified.

Characters 2 and 3 suggest a certain affinity with *Amia*, but the scales are wholly different. The dorsal fin is far posterior, about opposite the anal, as in the cyprinid genus *Engraulicypris*. In the adult the vertebral centra are solid, yet apparently always with a central canal for the notochord.

Doctor A. S. Woodward has described a second *Lycoptera*, *L. sinensis*, from the Lower Jurassic (?) of the Province of Shantung, China. Our specimens are, however, referable to *L. middendorffi*.

I think it is now evident that the Leptolepidæ of authors must be subdivided, at least to the following extent.

1.—Leptolepidæ. Marine (or sometimes brackish water ?) fishes, definable as indicated above,

a.—Leptolepinæ, new subfamily. Type *Leptolepis*, with scales as described above. (For other characters of these genera see Woodward.)

b.—Thrissopsinæ, new subfamily. Type *Thrissops*, with broad scales as described above. From the position of the dorsal fin opposite the anal, we might infer affinity with *Lycoptera*, but the scales are entirely different; so also the *Coryphæna*-like caudal fin.

2.—Lycopteridæ. Freshwater fishes, with scales resembling those of *Phoxinus*. *Lycoptera*, two species, or three if we include *Prolebias davidi* of Sauvage, 1880, from the supposed Tertiary of northern China.

Other genera referred to Leptolepidæ will have to be left in a rather uncertain position until their scales can be critically examined, but there is no indication that any one of them belongs to Lycopteridæ. In the Kimmeridge shale at Ringstead, Dorset, England, I collected circular or subcircular scales, 3 to 4 mm. diameter, with concentric circuli, strong annuli, and no radii. Doctor A. S. Woodward believes they must belong to Leptolepidæ, but they seem to represent a genus distinct from *Leptolepis dubius*.

PLATE III

Fig. 1. Enlarged figure of head of *Lycoptera middendorffi*. British Museum, P. 1841.

Fig. 2. Median dorsal scales of *Thrissops formosus*. Lithographic Stone, Solnhofen, Bavaria. British Museum, P. 913a.

Fig. 3. Anterior dorsal scales of *Leptolepis dubius*. Lithographic Stone, Solnhofen, Bavaria. British Museum, P. 924.

Figs. 4-8. *Lycoptera middendorffi*, from Ondai Sair.

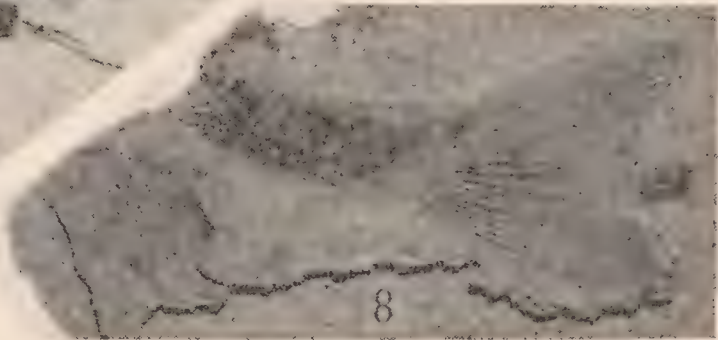
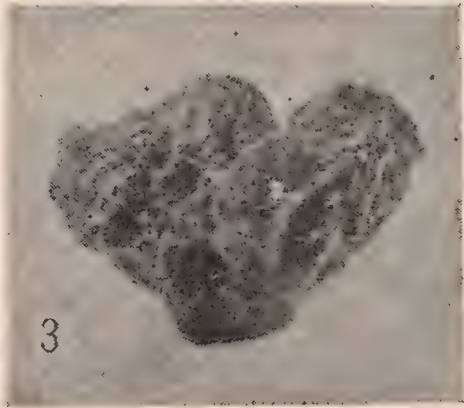
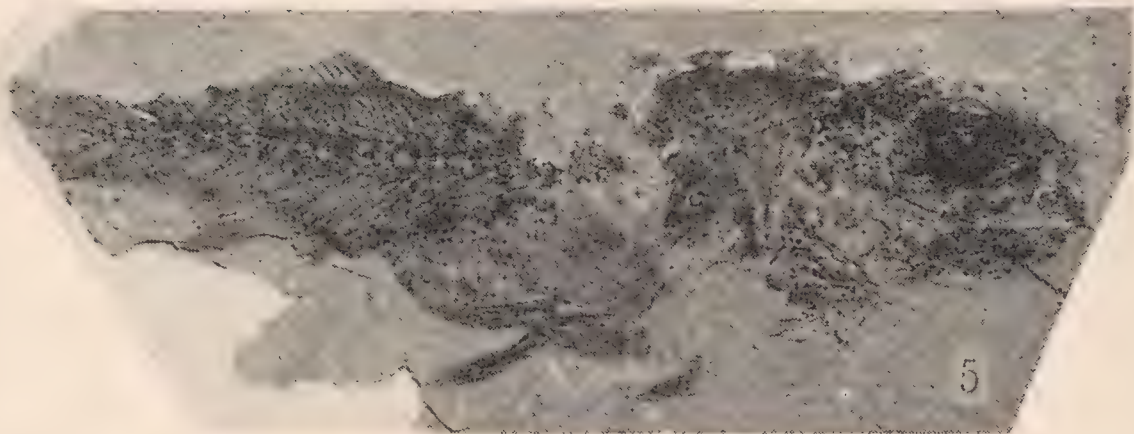
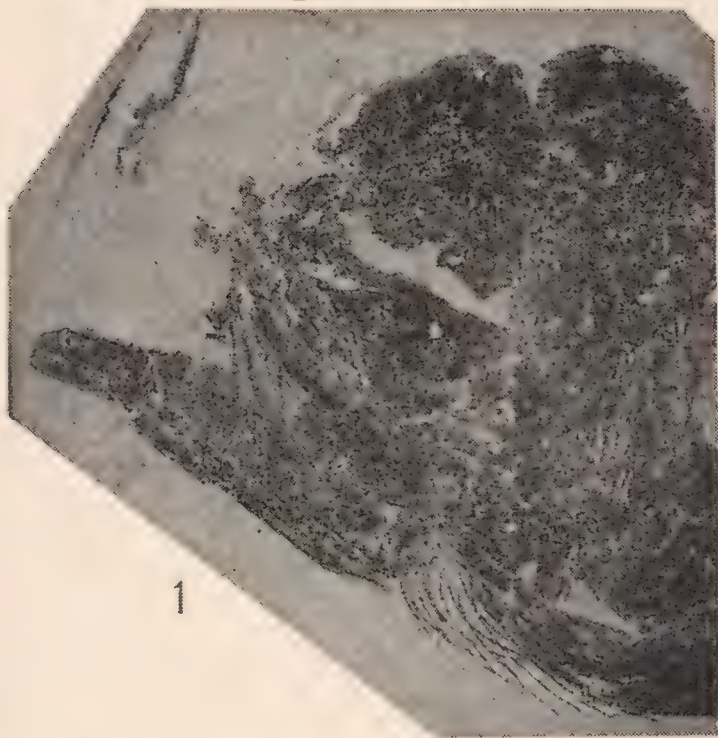
Fig. 4. General view of a small specimen.

Fig. 5. A larger specimen that preserves the head and pelvic fins fairly well.

Fig. 6. A large fish, in which the pectoral pelvic and anal fins are well preserved. The scales, shown in text figure 1, are drawn from the specimen.

Fig. 7. Well-preserved anal and part of a dorsal fin.

Fig. 8. A good caudal fin.



Article IX.—A REVISION OF THE MESOZOIC CROCODILIA OF NORTH AMERICA¹

PRELIMINARY REPORT

BY CHARLES C. MOOK

PLATES IV AND V; 63 TEXT FIGURES

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INTRODUCTION

This article contains material gathered in the preparation of a monographic revision of the fossil crocodilians of North America. The completion of this revision may be delayed indefinitely, and it has therefore been decided to publish the results of the preliminary investigations in the present form. The original references, as many of the later references as were available or were thought pertinent, and the original figures of all the genera and species of North American Mesozoic crocodilians have been brought together, along with statements of their geographic and geologic occurrences, the constitution and present disposition of the type specimens, and the original descriptions, quoted in full. In a few cases new figures were prepared under the writer's direction by Mr. John Germann.

No attempt has been made, at this stage of the work, to discuss the characters of the genera and species as they may be determined at the present time, and the determination indicated in each case after the citation of the original description is for the most part provisional. Further study will doubtless necessitate the changing of many of these determinations. Such a study cannot be satisfactorily made without careful and detailed comparison of the North American forms with those of Europe, Asia, Africa and South America. The purpose of the present report is to bring together in available form the present knowledge of the North American Mesozoic crocodilians.

The genera are treated chronologically in the order of their establishment, and under each genus the species are arranged chronologically.

GONIOPHOLIS Owen

ORIGINAL TYPE REFERENCE.—OWEN, R., 1842, 'Report on British Fossil Reptiles,' Rept. Brit. Assoc. Adv. Sci. Meeting at Plymouth (1841), II, pp. 69, 70.

SUBSEQUENT REFERENCES.—HULKE, J. W., 1878, 'Note on two Skulls from the Wealden and Purbeck Formations indicating a new Subgroup of Crocodilia,' Quart. Journ. Geol. Soc. London, XXXIV, pp. 377-381. OWEN, R., 1878, [Discussion of paper by J. W. Hulke on 'Note on two Skulls from the Wealden and Purbeck Formations indicating a new Subgroup of the Crocodilia'], Quart. Journ. Geol. Soc. London, XXXIV, p. 382; 1878, 'On the Influence of the Advent of a Higher Form of Life in Modifying the Structure of an Older and Lower Form,' Quart. Journ. Geol. Soc. London, XXXIV, pp. 421-430; 1878, 'Monograph on the Fossil Reptilia of the Wealden and Purbeck Formations. Supplement No. 8,' Palæontographical Soc., XXXII, pp. 1-10; 1879, 'Monograph on the Fossil Reptilia of the Wealden and Purbeck Formations. Supplement No. 9,' Palæontographical Soc., XXXIII, pp. 1-12. KOKEN, E., 1886, 'Über Gehirn und Gehör fossiler Crocodiliden vor,' Sitzber. Gesellsch. naturforsch. Freunde zu Berlin, No. 1, p. 2; 1888, 'Thoracosaurus macro-

rhynchus Bl. aus der Tuffkreide von Maastricht,' Zeitschr. d. Deutsch. Geol. Gesellsch. (Jahrg. 1888), pp. 754-773. LYDEKKER, R., 1888, 'Catalogue of the Fossil Reptilia and Amphibia in the British Museum,' Part 1, p. 79. NICHOLSON, H. A., AND LYDEKKER, R., 1889, 'A Manual of Palæontology for the Use of Students with a General Introduction on the Principles of Palæontology,' p. 1191. LYDEKKER, R., 1890, 'Catalogue of the Fossil Reptilia and Amphibia in the British Museum,' Part 4, p. 299. ZITTEL, K. VON, 1890, 'Handbuch der Palæontologie,' Abth. 1, Palæozoologie, III, Vertebrata, p. 676. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 516. HOLLAND, W. J., 1905, 'A New Crocodile from the Jurassic of Wyoming,' Ann. Carn. Mus., III, No. 3, Art. 9, pp. 431-434. WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol., XIV, pp. 3, 6-10, 12. LULL, R. S., 1907, 'The Reptilia of the Arundel Formation,' Maryland Geol. Surv., Lower Cretaceous, p. 177; 1907, 'Vertebrata,' Maryland Geol. Surv., Lower Cretaceous, p. 210.

TYPE.—*Goniopholis crassidens* Owen.

ORIGINAL TYPE DESCRIPTION.¹—"The second form of tooth having generic characters of those of the Crocodile, which has been discovered in the Wealden and approximate strata, is as remarkable for its thick, rounded and obtuse crown as the teeth of the preceding species [*Suchosaurus cultridens*] are for their slender, compressed, acute and trenchant character. It consequently approaches more nearly to the teeth which characterize the broad and comparatively short-snouted Crocodiles; but it differs from these in one of the same characters by which the tooth of *Suchosaurus cultridens* differs from those of the Gavials, viz. in the longitudinal ridges which traverse the exterior of the crown. These are, however, more numerous, more close-set, and more neatly defined than in the *Suchosaurus cultridens*. Two of the ridges, larger and sharper than the rest, traverse opposite sides of the tooth, from the base to the apex of the crown; they are placed, as in the Crocodile and Gavial, at the sides of the crown, midway between the convex and concave lines of the curvature of the tooth. These ridges are confined to the enamel; the cement-covered cylindrical base of the tooth is smooth. The size of the teeth varies from a length of crown of two inches, with a basal diameter of one inch and a half to teeth of one-third of these dimensions."

The genus may provisionally be considered valid.

***Goniopholis vebbianus* (Cope)**

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1872, 'On a new Testudinate from the Chalk of Kansas,' Proc. Amer. Phil. Soc., XII, p. 310, (*Hyposaurus vebbianus*).

SUBSEQUENT REFERENCES.—COPE, E. D., 1872, 'On the Geology and Paleontology of the Cretaceous Strata of Kansas,' Prel. Rept. U. S. Geol. Surv. of Montana and Portions of Adjacent Territories, F. V. Hayden in Charge, Fifth Annual Report, p. 327, (*Hyposaurus Vebbii*); 1874, 'Review of the Vertebrata of the Cretaceous Period found West of the Mississippi River,' Bull. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, I, No. 2, p. 26, (*Hyposaurus vebbii*); 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, pp. 52, 67, 68, 250, Pl. ix, figs. 8a, 8b, 8c, 8d, (*Hyposaurus vebbii*).

¹No distinction was made between generic and specific characters in Owen's original description, and the following extract is from the original description of *Goniopholis crassidens*.

MARSH, O. C., 1877, 'Notice of some New Vertebrate Fossils,' Amer. Journ. Sci. and Arts, (3) XIV, p. 254, (*Diplosaurus vebbii*). WILLISTON, S. W., 1898, 'Crocodiles,' Univ. Geol. Surv. Kansas, IV, Part 4, p. 78. ZITTEL, K. VON, 1890, 'Handbuch der Paläontologie,' Abth. 1, Paläozoologie, III, Vertebrata, p. 677, (*D.* [i.e., *Diplosaurus*] (*Hyposaurus*) *Vebbii* Cope). HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 516. WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol., XIV, No. 1, p. 7.

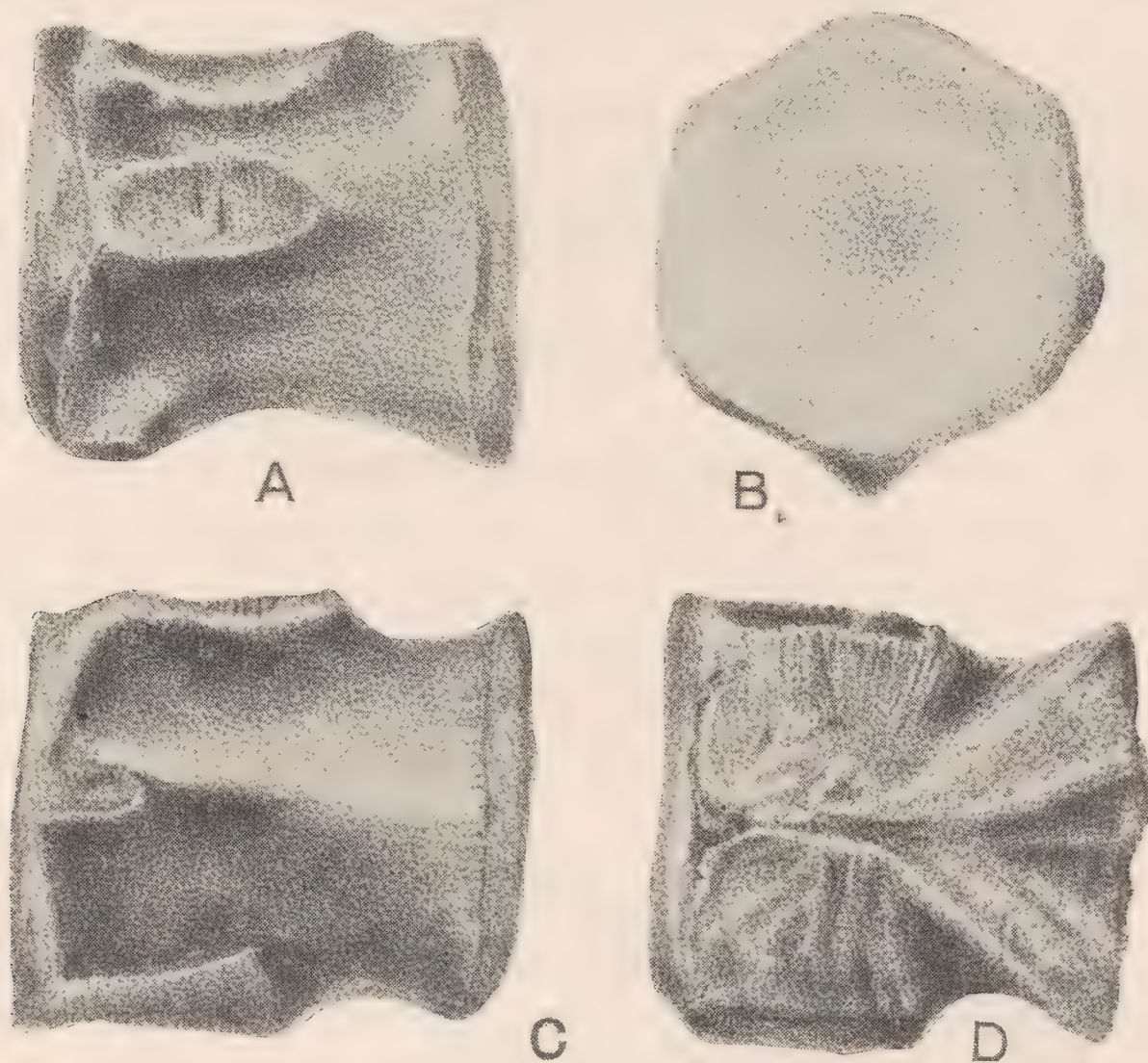


Fig. 1. *Goniopholis vebbii* (Cope). Type specimen, anterior cervical vertebra.

Two-thirds natural size. A, lateral view, left side; anterior view; C, inferior view; D, superior view. Original type figures. (After Cope.)

ORIGINAL TYPE FIGURES.—COPE, E. D., 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, Pl. IX, figs. 8a, 8b, 8c, 8d.

TYPE.—An anterior cervical vertebra.

TYPE LOCALITY AND LEVEL.—Brookville, Kansas. Benton Group, No. 20 of Meek and Hayden.

ORIGINAL TYPE DESCRIPTION.—"The crocodile may be called *Hyposaurus vebbii* in recollection of Dr. Wm. E. Webb, of Topeka; it is similar in size to the *H. rogersii* of New Jersey.

An anterior cervical presents the following characteristics: It is that one in which the parapophysis occupies a position opposite the lower third of the vertical diameter. In it the centrum is stout in form, the articular faces but little concave, the posterior a little more so than the anterior. The anterior is almost regularly

hexagonal, the posterior sub-round, a little deeper than wide. The inferior surface possesses a strong obtuse median carina, which disappears in front of the posterior margin. Anteriorly it terminates in a short obtuse hypapophysis. The suture of the neural arch is very coarse. Surface of the bone smooth.

			M.
Length of centrum.....			.037
Diameter, “	anteriorly, vertical.....		.037
“ “	“ horizontal.....		.031
“ “	posteriorly, vertically.....		.032
“ “	“ horizontally.....		.031
Length of surface of parapophysis.....			.015

As compared with the *H. rogersii* of the New Jersey Cretaceous, this vertebra is shorter and stouter, and the extremities less concave; the suture for the neural spine is much coarser.”

The species may provisionally be considered valid.

Goniopholis felix (Marsh)

ORIGINAL TYPE REFERENCE.—MARSH, O. C., 1877, ‘Notice of some New Vertebrate Fossils,’ Amer. Journ. Sci. and Arts, (3) XIV, p. 254, (*Diplosaurus felix*).

ORIGINAL TYPE REFERENCE.—MARSH, O. C., 1877, ‘Notice of some New Vertebrate Fossils,’ Amer. Journ. Sci. and Arts, (3) XIV, p. 254, (*Diplosaurus felix*).

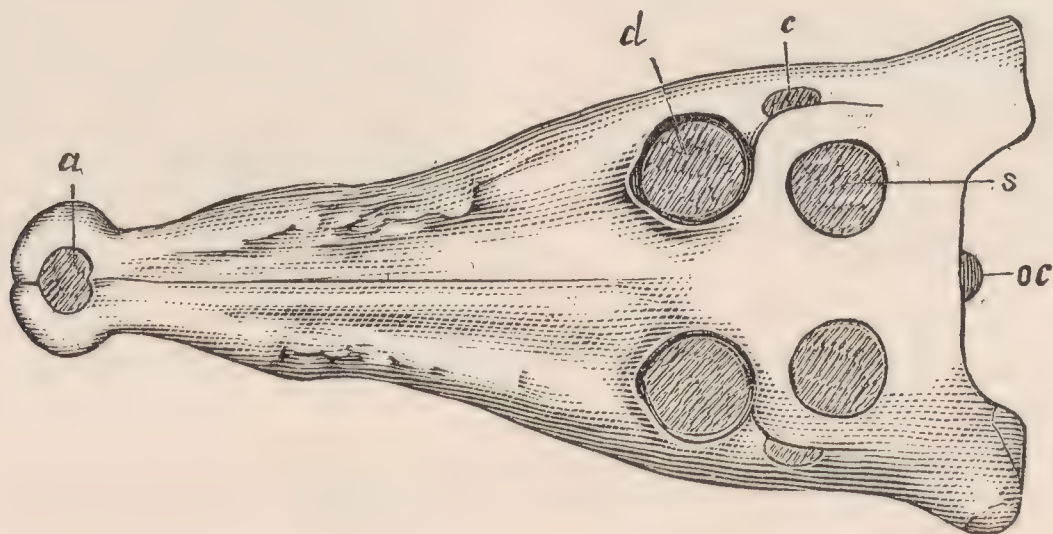


Fig. 2. *Goniopholis (Diplosaurus) felix* (Marsh).
Type specimen, skull (Yale Mus. Coll.).
One-fourth natural size. Superior view. Original type figure.
(After Marsh.)

SUBSEQUENT REFERENCES.—KING, C., 1878, ‘Systematic Geology,’ U. S. Geol. Explor. of the 40th Parallel, I, p. 346, (*Diplosaurus felix*). ZITTEL, K. VON, 1890, ‘Handbuch der Palæontologie,’ Abth. 1, Palæozoologie, III, Vertebrata, p. 677. MARSH, O. C., 1896, ‘A New Belodont Reptile (*Stegomus*) from the Connecticut River Sandstone,’ Amer. Journ. Sci., (4) II, p. 61, fig. 2, (*Diplosaurus felix*); 1897, ‘Vertebrate Fossils of the Denver Basin,’ U. S. Geol. Surv., Monograph XXVII, pp. 506, 507, fig. 62, (*Diplosaurus felix*). HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 516. WILLISTON, S. W., 1906, ‘American Amphicœlian Crocodiles,’ Journ. Geol., XIV,

No. 1, p. 7. LULL, R. S., 1910, 'Vertebrata,' Maryland Geol. Surv., Lower Cretaceous, p. 211. MOOK, C. C., 1916, 'A Study of the Morrison Formation,' Ann. N. Y. Acad. Sci., XXVII, p. 148.

ORIGINAL TYPE FIGURE.—MARSH, O. C., 1896, 'A New Belodont Reptile (*Stegomus*) from the Connecticut River Sandstone,' Amer. Journ. Sci., (4) II, p. 61, fig. 1; 1897, 'Vertebrate Fossils of the Denver Basin,' U. S. Geol. Surv., Monograph XXVII, p. 507, fig. 62.

TYPE.—Skull and vertebræ. Yale Museum.

TYPE LOCALITY AND LEVEL.—Near Morrison, Colorado. Morrison beds. Comanchean (possibly latest Jurassic).

ORIGINAL TYPE DESCRIPTION.—"An interesting discovery recently made in the lower Cretaceous, or Wealden beds, of Colorado, is a new genus of Crocodilians, intermediate between the old Teleosaurian type and the modern *Crocodylus*. The new genus has a head and teeth very similar to the latter, but with this the ancient biconcave vertebræ. The present type species is based upon a nearly perfect skull, and a number of vertebræ belonging with it. These pertained to an animal smaller than most existing Crocodilians.

Some of the principal measurements of this species are as follows:

Length of skull on median line.....	255. mm.
Length of skull from quadrate to end of snout....	275.
Transverse diameter of premaxillaries.....	46.
Transverse diameter of skull, at front of orbits....	90.
Transverse diameter at ends of quadrates.....	122.
Transverse diameter of quadrate at end.....	20.

A second species of this genus is apparently the *Hyposaurus Vebbii* Cope, which may be called *Diplosaurus Vebbii*."

The species may provisionally be considered valid.

***Goniopholis lucasii* (Cope)**

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1878, 'Descriptions of New Extinct Vertebrata from the Upper Tertiary and Dakota Formations,' Bull. U. S. Geol. and Geog. Surv. Terr., F. V. Hayden in Charge, IV, No. 2, pp. 391, 392, (*Amphicotylus lucasii*).

SUBSEQUENT REFERENCES.—COPE, E. D., 1888, 'Goniopholis in the Jurassic of Colorado,' Amer. Nat., XXII, pp. 1105, 1106. ZITTEL, K. VON, 1890, 'Handbuch der Palæontologie,' Abth. 1, Palæozoologie, III, Vertebrata, p. 677, ((*D. (Goniopholis lucasi*)). HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 516. WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol., XIV, p. 7. MOOK, C. C., 1916, 'A Study of the Morrison Formation,' Ann. N. Y. Acad. Sci., XXVII, p. 148.

ORIGINAL TYPE FIGURE.—No figure of the type has been published.

TYPE.—Dorsal and lumbar vertebræ, ribs and dermal bones. Amer. Mus. Cope Coll. No. 5766.

TYPE LOCALITY AND LEVEL.—Garden Park, near Canyon City, Colorado. Morrison beds of Comanchean or possibly uppermost Jurassic age.

The premaxillaries have not sustained much crushing; the anterior edge has been broken, and the margin of these bones is not entire. A portion of the posterior



Fig. 3. *Goniopholis gilmorei* Holland. Type specimen, skull (Carn. Mus. No. 1339).

Two-fifths natural size. Superior view. Original type figure. (After Holland. The portions marked + have been restored.)

margin of the right dental foramen is, however, preserved, showing that the animal possessed the dental foramina, and thus was allied to the genus *Crocodylus* rather than to the genus *Alligator* Cuvier, or the genus *Gavialis* Oppel, the former of which is characterized by the absence of the dental foramina, except possibly in extreme age, and the latter of which is always without these openings. The foveæ on the lower surface of the intermaxillaries which lead from the orifices of the dental foramina are distinctly marked on the under surface of the skull. The snout is strongly constricted at the point where the premaxillaries unite with the maxillaries at the dental incisure. The nasal bones do not reach the narial opening, their anterior ends terminating between the premaxillaries fully three centimeters from the posterior margin of this opening. The alveolar border of the maxillaries extends backward from the point of union with the premaxillaries, in a widening curve, to a point in advance of the orbital cavities. There does not appear to be much, if any, evidence of lateral compression of the skull about the middle of the maxillaries, as is the case in the skull of many species of recent crocodiles, notably *Crocodylus Americanus* Seba. The distortion of the specimen to which the skull has been subjected as the result of vertical pressure may have slightly obliterated the evidence of constriction at the point indicated, in case it existed in life.

The arrangement of the bones composing the roof of the back part of the skull is essentially like that in the recent genus *Crocodylus*. At the point where the mastoid and the parietal bone form the inner and posterior margins of the supratemporal fossæ there are developed well marked convex bony ridges, rising about four mm. in height above the plane of the upper surface of the bones which have been named. This bony ridge is far more strongly marked than in the recent genus *Crocodylus*, where it exists only as a vestige. In other respects the upper surface of the skull shows no points of difference from modern types. The under surface of the specimen preserves, though greatly crushed, the outlines of the bones of the inferior surface of the skull, and these do not seem to diverge in form and arrangement from well known recent types.

With the skull were associated a few teeth. The alveolar border of the maxillaries and premaxillaries is sufficiently perfect to show that the number of teeth was identical with that of the modern genus *Crocodylus*, and the arrangement of the teeth and their relative sizes, so far as it is possible to ascertain the facts from the skull under consideration, was the same as in *Crocodylus*. Three successional teeth are preserved on the left hand side of the upper jaw, and the crowns of two larger teeth were found detached from the skull and in the matrix beside it, evidently belonging to the same specimen. These teeth differ somewhat from those of the recent genus *Crocodylus* in being somewhat more compressed and trenchant and not as conical. They are not, however, as obtuse as the teeth described by Owen as belonging to the genus *Goniopholis*, although upon the crown, particularly upon the inner surface, they distinctly reveal the neatly defined longitudinal ridges, which appear to agree with the description given by Owen. The two lateral ridges, one anterior and the

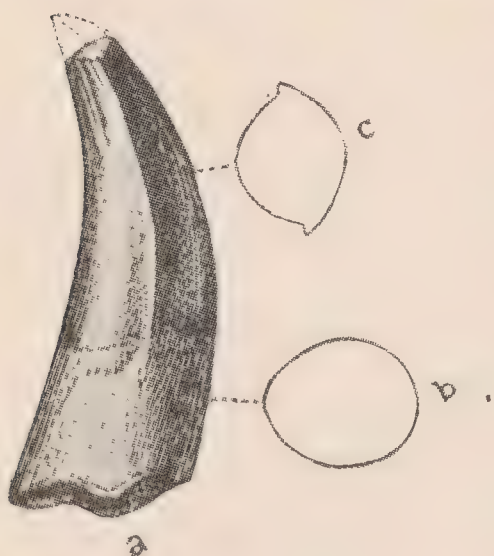


Fig. 4. *Goniopholis gilmorei* Holland. Type specimen, teeth (Carn. Mus. No. 1339).

Natural size. a, lateral view; b, outline of section at base; c, outline of section at middle of crown. Original type figure. (After Holland.)

other posterior, midway between the convex and concave surfaces, are in both cases sharply defined, and even more sharply than in the genus *Crocodilus*. The larger of the teeth that have been preserved appears to the writer to be, reckoning from the front, No. 10 in the left series.

DIMENSIONS OF THE SKULL OF GILMORE'S CROCODILE			
Length of skull on median line.....		38.50	cm.
“ “ “ from posterior extremity of quadrate to end of snout.....		44.50	“
Transverse diameter of snout across premaxillaries.....		7.20	“
“ “ “ at junction of maxillaries and premaxil-			
laries.....		4.00	“
“ diameter of skull at front of orbits.....		10.80	“
“ “ “ at upper ends of mastoids.....		12.00	“
“ “ “ at end of quadrates.....		20.00	“
Longitudinal diameter of left orbital foramen.....		4.00	“
Transverse “ “ “ “ “		5.20	“
Longitudinal “ “ “ postorbital foramen.....		4.50	“
Transverse “ “ “ “ “		3.50	“
Diameter of supratemporal foramen.....		4.00	“

The specific characters by which this species may be distinguished from the other species of the genus *Goniopholis* described from North America appear to be the very closely pitted superior surface of the bones of the skull, the existence of the elevated ridges partly surrounding the supratemporal foramina, and the less obtuse, elongated and compressed shape of the teeth.

The writer assigns the species to the genus *Goniopholis* with doubt: first, because no vertebræ were collected, and therefore it is unknown whether the centra were amphiœlous as in *Goniopholis* or not; and, secondly, because the longer, less obtuse, and more trenchant teeth do not fully accord with the generic description given by Owen.”

The species may provisionally be considered valid.

Goniopholis affinis Lull

ORIGINAL TYPE REFERENCE.—LULL, R. S., 1910, ‘The Reptilia of the Arundel Formation,’ Maryland Geol. Surv., Lower Cretaceous, pp. 177, 210, 211; ‘Vertebrata,’ same volume, pp. 210, 211, Pl. xx, fig. 7.

SUBSEQUENT REFERENCE.—GILMORE, C. W., 1921, ‘The Fauna of the Arundel Formation,’ Proc. U. S. Nat. Mus., LIX, p. 589, Pl. cx, fig. 1 (Pub. 2389).

ORIGINAL TYPE FIGURE.—LULL, R. S., 1910, Maryland Geol. Surv., Lower Cretaceous, Pl. xx, fig. 7.

TYPE.—A tooth. Maryland Geol. Surv. No. 8175 according to Lull; U. S. Nat. Mus. No. 8452 according to Gilmore.

TYPE LOCALITY AND LEVEL.—Branchville, Prince George’s County, Maryland. Arundel formation.

ORIGINAL TYPE DESCRIPTION.—“The fauna includes a crocodile, *Goniopholis*, found in the Wealden and Purbeck beds of Europe and in the Morrison of Colorado and Wyoming. The teeth are so similar to those from the western quarries that the name *Goniopholis affinis*, the nearly related, is given to the Potomac type. These are

crocodiles of moderate size, 6 feet or more in length, and may have resembled the modern genus *Crocodylus*, with its narrow snout, quite closely in general appearance.



Fig. 5. *Goniopholis affinis* Lull. Type specimen, tooth (Md. Geol. Surv. No. 8175, U. S. Nat. Mus. No. 8452).

Natural size. Edge view. Original type figure. (After Lull.)

A crocodile is represented by a number of teeth and part of a scute. The teeth, however, are the most distinctive. They show beyond question the generic characters of *Goniopholis*: 'stout, rounded, slightly curved, with the enamel ridged and grooved, and well-marked carinæ placed in a 'plane coincident with that of the curvature of the crown'. . . They resemble very closely a multitude of teeth from 'Quarry 9,' Como, Wyoming (Morrison); preserved in the Yale Museum, which agree in size with those of the type specimen of *Goniopholis* (*Diplosaurus*) *felix* (Marsh). Unfortunately, none of the crowns in the last specimen show their outer surface, but those of the Maryland specimen differ from those from Como by having secondary ridges between the main ridges on the proximal portion of the crown. See figure. The similarity aside from this feature is very great and shows a close relationship with the Morrison type as the specific name implies. The sculpturing on the scute (No. 5465) is coarser than on any of those in the lot of material from Como. This may, however, be due to the portion of the body from which the scute came, and is probably not of importance.

Tooth No. 8175, M. G. S., may be taken as type.

Length of crown about.....25 mm.

Width of crown at base.....12 mm."

According to Gilmore, this species cannot be considered as determinate. It is possible that, in spite of the fragmentary nature of the type, distinctive characters may be found on further study of the type material. No further determination can be made at the present time, however.

BOTTOSAURUS Agassiz

ORIGINAL TYPE REFERENCE.—AGASSIZ, L., 1849, [Remarks on the Crocodilia of the Greensand of New Jersey and on *Atlantochelys*], Proc. Acad. Nat. Sci. Phila., IV, p. 169.

SUBSEQUENT REFERENCES.—LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, p. 12. COPE, E. D., 1869, 'The Fossil Reptiles of New Jersey,' Amer. Nat., III, p. 90; 1869, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N. S., XIV, Part 1, Art. 1, pp. 62, 65. MARSH, O. C., 1877, 'Introduction and Succession of Vertebrate Life in America,' Amer. Journ. Sci. and Arts, Ser. 3, XIV, Art. 42, p. 346. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krododil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch, Wien, p. 354. LYDEKKE, R., 1886, 'Siwalik Crocodilia, Lacertilia, and Ophidia,' Mem. Geol. Surv. India, Palæontologia Indica, Ser. 10, III, Part 7, p. 3 (211). ZITTEL, K. VON, 1890, 'Handbuch der Palæontologie,' Abth. I, Palæozoologie, III, Vertebrata, p. 679. WILLISTON, S. W., 1906, 'American Amphicælian Crocodiles,' Journ. Geol., XIV, pp. 2-4. GILMORE, C. W., 1910, 'Leidyosuchus sternbergii, a New Species of Crocodile

from the Ceratops Beds of Wyoming,' Proc. U. S. Nat. Mus., XXXVIII, p. 492 (Pub. No. 1762); 1911, 'A New Fossil Alligator from the Hell Creek Beds of Montana,' Proc. U. S. Nat. Mus., XLI, pp. 297, 298 (Pub. No. 1860).

TYPE.—*Crocodylus macrorhynchus* Harlan = *Bottosaurus harlani* Meyer.

ORIGINAL TYPE DESCRIPTION.—"Professor Agassiz made some remarks on the distinctions between the fossil Crocodiles of the green sand of New Jersey, described by Drs. Harlan and Morton, and characterized that of Dr. Harlan as a distinct genus under the proposed name of *Bottosaurus*." (Minutes of meeting of Academy of Natural Sciences of Philadelphia for March 6, 1849).

The genus may provisionally be considered valid, though it requires further study to determine its characteristics.

***Bottosaurus harlani* (Meyer)**

ORIGINAL TYPE REFERENCES.—HARLAN, R., 1824, 'On an Extinct Species of Crocodile not before described; and some Observations on the Geology of West Jersey,' Journ. Acad. Nat. Sci. Phila., IV, pp. 15-24, Pl. I ("Crocodile," no species name indicated). MEYER, H. VON, 1832, 'Palæologica,' p. 108 (name "Harlani" with no generic reference or description).

SUBSEQUENT REFERENCES.—HARLAN, R., 1834, 'Critical Notices of Various Organic Remains hitherto discovered in North America,' Trans. Geol. Soc. Pennsylvania, I, Part 1, pp. 76, 77; also 1835, 'Med. and Phys. Res.,' pp. 280, 281, (*Crocodylus macrorhynchus*); also 1835, Edinburgh New Phil. Journ., XVII, between pp. 342 and 362, pp. 29, 40, [not seen]; 1835, 'Description of an Extinct Species of Crocodile, not before described; and some Observations on the Geology of West Jersey,' in 'Med. and Phys. Res.,' pp. 378-380, 1 Pl., (*Crocodylus macrorhynchus*); also 1836, Translation into German, Neues Jahrb. f. Min., Geognos., Geol. u. Petrefakt., p. 105. DE KAY, J., 1842, 'Zoology of New York,' Part 3, p. 27, (*Crocodylus macrorhynchus*). GIEBEL, C. G., 1847, 'Fauna der Vorwelt,' II, p. 122, (*Crocodylus macrorhynchus*). GIBBES, R. W., 1851, 'Memoir on *Mosasaurus* and Three Allied new Genera, *Holcodus*, *Conosaurus*, and *Amphorosteus*,' Smith. Contrib. Knowl., II, Art. 5, p. 7, (*Crocodylus macrorhynchus*). LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, pp. 12-14, 115, Pl. IV, figs. 19-23, Pl. XVIII, figs. 11-14. COPE, E. D., 1867, 'The Fossil Reptiles of New Jersey,' Amer. Nat., I, p. 26; 1869, 'Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,' in 'Geology of New Jersey,' by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736; 1869, 1870, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N. S., XIV, pp. 65-67, (1869), p. 231 (1870); 1871, 'Supplement to the Synopsis of the Extinct Batrachia and Reptilia of North America,' Proc. Amer. Phil. Soc., XII, pp. 48-50, (*Bottosaurus macrorhynchus*). LEIDY, J., 1782, 'Brief Review of a Memoir on the Cretaceous Reptiles of the United States, published in the Fourteenth Volume of the Smithsonian Contributions to Knowledge,' Ann. Rept. Board of Regents Smith. Inst., for 1866, pp. 67, 68. COPE, E. D., 1874, 'Review of the Vertebrata of the Cretaceous Period found west of the Mississippi River,' Bull. U. S. Geol. and Geog. Surv. Terr., F. V. Hayden in Charge, I, No. 2, first series, p. 27, (*Bottosaurus macrorhynchus*); 1874, 'Report on the Vertebrate Paleontology of Colorado,' Ann. Rept. U. S. Geol. and Geog. Surv. Terr. (for 1873), F. V. Hayden in Charge, p. 452, (*Bottosaurus macrorhynchus*);

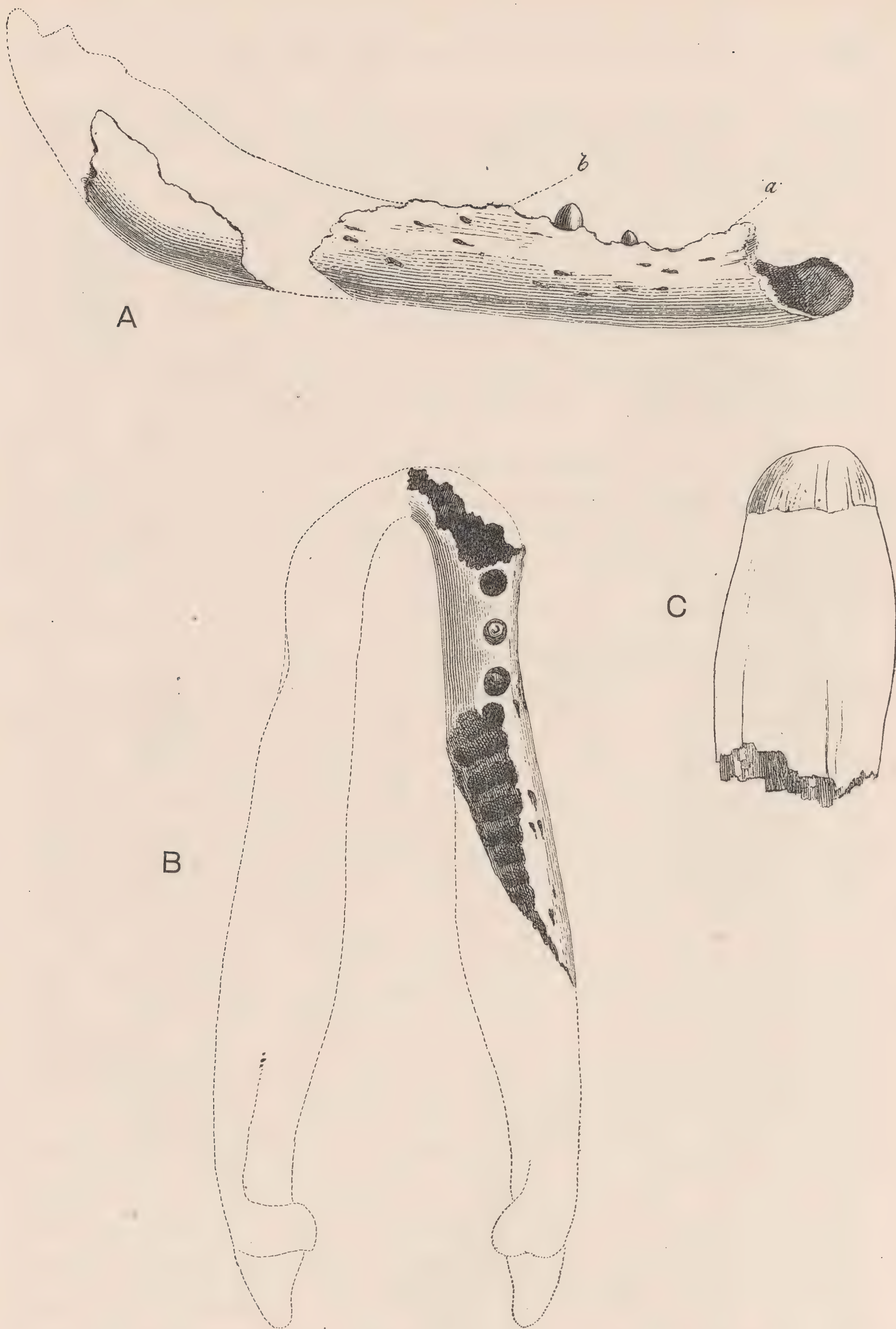


Fig. 6. *Bottosaurus harlani* (Meyer). Type specimen, portions of dentary and angular bones, and paratype specimen, tooth (Acad. Nat. Sci. Phila. Coll.).

A, portions of right dentary and angular bones, with outline restoration of jaw, external view, about one-sixth natural size; B, portion of dentary bone, with outline restoration of jaw, superior view, about one-sixth natural size; C, tooth, external view, natural size. Original type figures. (After Harlan.)



Fig. 7. *Bottosaurus harlani* (Meyer). Type specimens, right dentary and angular bones (Acad. Nat. Sci. Phila. Coll.).

One-third natural size. A, superior view of dentary; B, external view of same; C, external view of angular. (After Leidy.)

1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, pp. 68, 253, (*Bottosaurus macrorhynchus*); TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354, (*Crocodylus harlani*). HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 514. WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol., XIV, No. 1, p. 3. LAMBE, L. M., 1907, 'On a New Crocodilian Genus and Species from the Judith River Formation of Alberta,' Trans. Roy. Soc. Canada, Ser. 3, I, p. 220. GILMORE, C. W., 1911, 'A New Fossil Alligator from the Hell Creek Beds of Montana,' Proc. U. S. Nat. Mus., XLI, pp. 297, 299 (Pub. No. 1860).

ORIGINAL TYPE FIGURES.—HARLAN, R., 1824, 'On an Extinct Species of Crocodile not before Described; and some Observations on the Geology of West Jersey,' Journ. Acad. Nat. Sci. Phila., Pl. I, figs. 1, 2, 8.

TYPE.—Portion of a right dentary bone with portion of angular. Paratype: teeth. Acad. Nat. Sci. Phila. Coll.

TYPE LOCALITY AND LEVEL.—Three miles from White Hill, New Jersey. Upper Cretaceous Greensands.

ORIGINAL TYPE DESCRIPTIONS.—"The fossil, under consideration, is the dental bone of the right side, in a tolerable state of preservation, perfectly fossilized or impregnated with iron, containing the sockets for eleven teeth, in a space of twelve inches; three of the teeth only remain perfect, a portion of the bone is lost posteriorly and interiorly; consequently the total number of teeth cannot be ascertained with perfect accuracy; though, from the great size of the inferior maxillary foramen immediately behind the last remaining tooth, there could not have existed more than

one or two more at most. A portion of the angular bone was fortunately preserved, which will enable us to determine the form of the angle, and thus to reconstruct, with sufficient accuracy, the whole of the lower jaw.

The most striking peculiarity of this remnant is its great thickness in proportion to its length, compared with the same part in other crocodiles; with which circumstance the structure and appearance of the teeth perfectly correspond; being exceedingly short, thick and blunt, except the very young tooth, which is sharper and more conical.

In the *CROCODYLUS ACUTUS*, a portion of the dental bone, eight inches in length, contains ten teeth; the same measurement taken from the *CROCODYLUS LUCIUS*, thirteen and a half feet

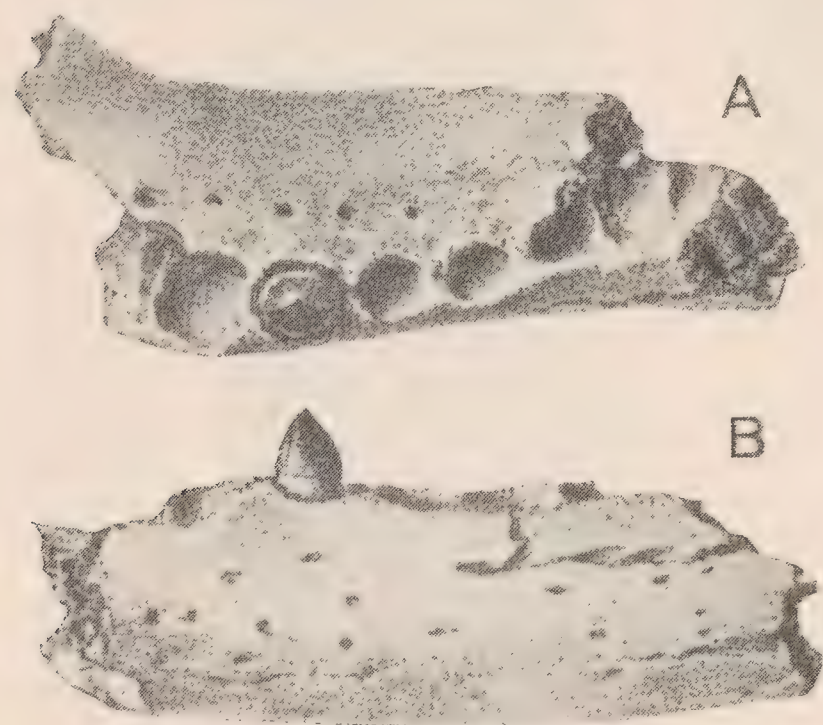


Fig. 8. *Bottosaurus harlani* (Meyer). Left dentary, young individual from Monmouth County, New Jersey.

One-half natural size. A, superior view; B, external view. (After Leidy.)

long, affords space for thirteen teeth. In our fossil, on the contrary, there is only space allowed for seven teeth; in every instance commencing from the fourth tooth, and enumerating backwards.

In the *C. acutus*, the dental bone, immediately behind the fourth tooth, is one inch, four-tenths, in breadth. In the *C. lucius*, one inch, seven-tenths. In the fossil, two inches, four-tenths. Depth of the same portion of bone, in the *C. acutus*, is one inch, two-tenths; in the *C. lucius*, two inches; in the fossil, two inches, five-tenths. By this measurement, the fossil bone is shown to be nearly cylindrical.

The teeth of the fossil, though very short and thick, are not much worn—the largest tooth of the lower jaw, in the *C. lucius*, thirteen feet long, is twenty-four tenths in circumference; the largest of the fossil teeth is thirty-three tenths. Of one of the loose fossil teeth, the length is two inches; diameter one inch; whilst the portion which projected above the bone, is only half an inch long. The caliber of the tooth at its base is half an inch in diameter. The bodies of the teeth are separated by a plate of bone only four or five-tenths in thickness.

The anterior or alveolar portion of the lower jaw, in all the Crocodiles excepting Cuvier's sub-genus *C. gangeticus*, presents a series of vertical curvatures; there are three in number in the fossil, in which respect it resembles the recent Crocodiles and Alligators; but which will alone separate it from the Gavials as well as all the fossil specimens hitherto discovered, which most nearly resemble the Gavials; in all of which this portion of the jaw is straight; but the present species is still further separated from all the sub-genera of Cuvier, by the greater relative thickness and less length of the dental bone, as well as in the peculiarities of the teeth above-mentioned. The space between the fourth tooth and greatest elevation of the dental bone, in the fossil (a.b.) contains five teeth; in the *C. lucius*, nine; in the *C. acutus*, six.

The distance from the fourth tooth, (which is very large proportionably) to the anterior margin of the symphysis in the fossil, is four inches, two-tenths; in the *C. lucius*, two inches, seven-tenths; in the *acutus*, two inches, six-tenths. The symphysis of the lower jaw extends posteriorly to the fourth tooth in the *C. acutus*; it terminates two inches anteriorly in the fossil; its termination is nearly

opposite the fourth tooth in the *C. lucius*. Directly posterior to the fourth tooth, there exists a considerable curvature inwards, in the fossil; directly the reverse is the case in the *C. lucius*; but a similar curvature exists in a very slight degree in the *C. acutus*.

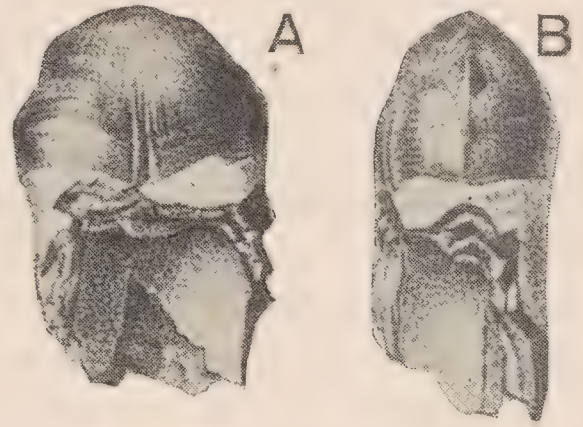


Fig. 9. *Bottosaurus harlani* Meyer. Paratype specimen, tooth (Acad. Nat. Sci. Phila. Coll.).

Natural size. A, external view; B, lateral view. (After Leidy.)

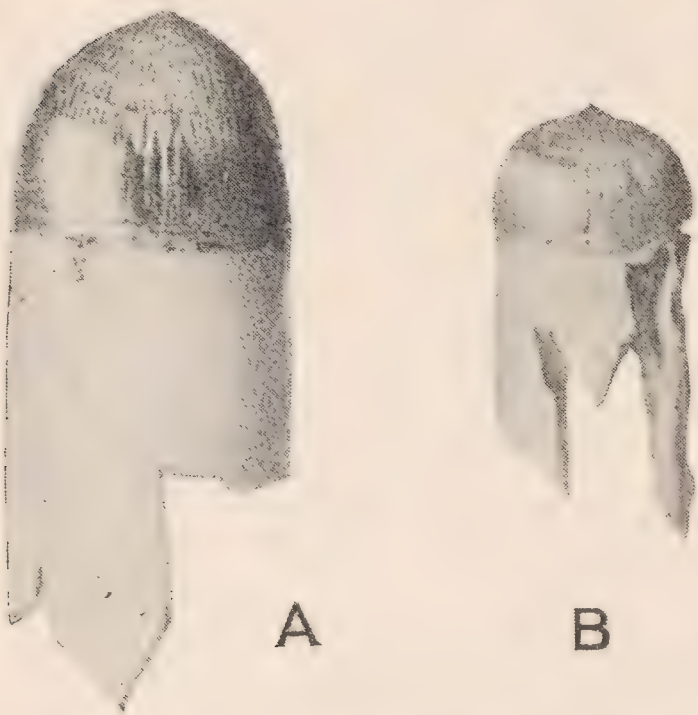


Fig. 10. *Bottosaurus harlani* (Meyer). Teeth referred by Leidy to this species.

A (Burlington County Lyceum of Natural History Coll.), large tooth, external view, natural size; B, small tooth (collection not known), external view, natural size. (After Leidy.)

The foramina for the transmission of nerves and blood-vessels are unusually large and numerous in the fossil. By referring to the figures, other differences will be noticed equally remarkable, though not so readily expressed; all of which, taken collectively, constitute, in my opinion, characters sufficient to require for this animal the establishment of a new subgenus.

I am not, as yet, prepared to answer positively to the question, did this animal exist in salt or fresh water? As far as my information extends, no fossil Crocodile has hitherto been discovered in salt water formation. The pretended Crocodiles, said to have been found with fish in the pyritose schistus of Thuringia, are evidently Monitors, as has been demonstrated by Cuvier. However, the form of the teeth, great thickness, and strength of the jaws, in the present instance, would qualify this species to crush shell-fish, &c. and defend itself against powerful enemies.

Numerous vertebræ of Crocodiles have been found in the same locality, none of which, however, are large enough to have belonged to this individual, but very different from any I have been able to compare them with; though very much broken, yet this difference is readily recognized by a very peculiar compression of the lateral and inferior portion of the bodies; as might be anticipated, the vertebræ, already discovered, denote a variety of species." (Harlan).

(Meyer) "—Harlani." No description.

The species may be considered valid.

Bottosaurus (Crocodilus) macrorhynchus Harlan

ORIGINAL TYPE REFERENCES.—HARLAN, R., 1824, 'On an Extinct Species of Crocodile not before described; and some Observations on the Geology of West Jersey,' Journ. Acad. Nat. Sci. Phila., IV, pp. 15–24, Pl. 1, ("Crocodile," no specific name); 1834, 'Critical Notices of Various Organic Remains Hitherto Discovered in North America,' Trans. Geol. Soc. Pennsylvania, I, Part 1, pp. 76, 77; also 1835, 'Med. and Phys. Res.,' pp. 280, 281, (*Crocodilus macrorhynchus*).

SUBSEQUENT REFERENCES.—HARLAN, R., 1835, 'Description of an Extinct Species of Crocodile, not before Described, and some Observations on the Geology of West Jersey,' in 'Med. and Phys. Res.,' pp. 378–380, 1 Pl., (*Crocodilus macrorhynchus*). DE KAY, J. E., 1842, 'Zoology of New York,' Part 3, p. 27. GIEBEL, C. G., 1847, 'Fauna der Vorwelt,' II, p. 122, (*C. macrorhynchus*). GIBBES, R. W., 1851, 'Memoir on *Mosasaurus* and Three Allied New Genera, *Holcodus*, *Conosaurus*, and *Amphorosteus*,' Smith. Contrib. Knowl., II, Art. 5, p. 7, (*Crocodilus macrorhynchus*). COPE, E. D., 1871, 'Supplement to the Synopsis of the Extinct Batrachia and Reptilia of North America,' Proc. Amer. Phil. Soc., XII, p. 48; 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, pp. 68, 253. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 514. WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol., XIV, p. 3, (*Crocodilus macrorhynchus*).

ORIGINAL TYPE FIGURES.—HARLAN, R., 1824, 'On an Extinct Species of Crocodile not before Described; and some Observations on the Geology of West Jersey,' Journ. Acad. Nat. Sci. Phila., IV, Pl. 1, figs. 1, 2, 8.

TYPE.—Portion of right dentary bone, with portions of angular. Paratype: Teeth. Acad. Nat. Sci. Phila. Coll. The type of *Bottosaurus harlani* Meyer.

ORIGINAL TYPE DESCRIPTION.¹—"Several fine specimens of the jaw, teeth, vertebræ &c. of an extinct fossil species of crocodile from the New Jersey marl-pits, . . . are contained in the Cab. of the Ac. Nat. Sciences; the most perfect of these is described and figured as above referred to. It consists of the dental bone of the right side, in a good state of preservation, perfectly fossilized, or impregnated with iron, so abundant in the marl-pits of New Jersey; it contains the sockets of eleven teeth in a space of twelve inches.

The most striking peculiarity of this remnant is its great thickness in proportion to its length, compared with the same part in recent crocodiles, with which circumstance the structure and appearance of the teeth perfectly correspond, being exceedingly thick, short, and blunt. Length of one of these teeth, two inches, diameter at base one inch; only one-half an inch projecting beyond the alveole."

Since this species was based upon the type of *Bottosaurus harlani* Meyer, and named later, it is clearly a synonym of that species.

***Bottosaurus tuberculatus* Cope**

ORIGINAL TYPE REFERENCE.¹—COPE, E. D., 1869, 1870, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N. S., XIV, Part 1, pp. 65, 230, 231, (p. 65, referred to *B. harlani* Meyer; pp. 230, 231, *B. tuberculatus*).

SUBSEQUENT REFERENCES.—COPE, E. D., 1871, 'Supplement to the Synopsis of the Extinct Batrachia and Reptilia of North America,' Proc. Amer. Phil. Soc., XII, pp. 48, 49. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Acad. Wissensch. Wien, p. 354. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 514.

ORIGINAL TYPE FIGURE.—No figure of the type has been published.

TYPE.—Twenty-seven vertebræ from the dorsal, lumbar, sacral and caudal series, with large portions of the pelvis and both hind limbs, including two perfect femora; also, about fifty dermal bones.

TYPE LOCALITY AND LEVEL.—Near Birmingham, New Jersey. Greensands, Upper Cretaceous.

ORIGINAL TYPE DESCRIPTION.—"From an examination of additional material, I am disposed to believe that the *Bottosaurus*, described under the head of *B. harlani*, at page 65, as a smaller individual, really represents a different species which I name above. The material is from the same locality as the above specimen, and consists of twenty-seven vertebræ from the dorsal, lumbar, sacral and caudal series, with large portions of the pelvis and both hind limbs, including two perfect femora; also, about fifty dermal bones.

Cranium and teeth. These are described as above. The acute, conic dental crown, which, I at one time referred to the position of canine of *B. harlani*, I believe to indicate the specific distinctness of the present animal. The specimen of the latter appears to be mature, as one half the neural arches of the vertebræ are coössified; the size is, therefore, not more than half that of *B. harlani*.

¹Harlan's original description of the material is given under *Bottosaurus harlani*.

Vertebræ. A prominent character to be noticed is that none of the dorsal and lumbar series has compressed centrum, as is the case with most of the *Holopes*; nor have any of the posterior dorsals the compression seen in *H. obscurus*. Second, the centra never present the parallelogrammic horizontal section seen in the *Holopes*; on the contrary, they are much contracted just in front of the articular ball, and flare out regularly laterally, to the rim of the socket. The lip of the cup is thin, and the cup inclines to narrow downward, especially anteriorly. This is owing to the fact that the inferior median line becomes pinched or narrowed on approaching the position of the hypapophysis. One vertebra with the latter is preserved; the process is broken off, but had a small basis,

	<i>Lines.</i>		<i>Lines.</i>
Width cup first lumbar,	21.2	Width neural canal,	7.4
“ “ “	17	Antero-posterior length between	
		ends of zygapophyses,	34
Length centrum,	28.6	Expanse of anterior pair of do.,	45
Width cup fifth dorsal,	20.	Width neural canal	6.8
“ “ “	16.5	Antero-posterior spread of zygapo-	
		physes,	33.4
Length centrum do.,	27	Expanse of anterior do.,	38.2

The *Femora* are large in proportion to the size of the *vertebræ*. The head exhibits the round form characteristic of *Holops*, not the obliquity of *Hyposaurus*. What characterizes it is the great prominence of the ridge, rudimental in the latter, which represents the third trochanter of *Dinosauria*. This prominence is increased by the presence both anteriorly and posteriorly of a strongly marked pit. Another marked characteristic, not seen in other genera, is the truncation of the posterior margin of the shaft close to the head, down to nearly opposite the third trochanter; the surface thus produced is deeply grooved. Inside of the head roughly grooved; outside flatter, more finely grooved; a grooved swell, in the position of the great trochanter of other forms. The shaft, compared with the *Holopes* and *Hyposaurus*, figured in the present work (Pl. IV.), is shorter and more curved. The condyles are wide, with narrow posterior prolongations extending on each side of a wide and deep popliteal groove.

	<i>In.</i>	<i>Lin.</i>		<i>In.</i>	<i>Lin.</i>
Length of right femur,	10	8	Expanse condyles,	2	8.6
Width head,	2	9.8	Circumference shaft at middle,	4	4.
Length to 3rd trochanter,	3	11.7			

The *tibia* is stout and slightly curved; the condyloid extremity presents two articular surfaces at right angles to one another, of which the longer is contracted in respect to the length of the bone, and is supported by a thin margin. The proximal extremity is broken from that of one side, but remains with a part of the shaft of the other.

	<i>In.</i>	<i>Lin.</i>		<i>Lin.</i>
Length (not restored,)	7	11	Diameter median,	14
Diameter proximal,	1	10	“ distal,	26

Portions of shafts, etc., of most of the other long bones are preserved.

Both *ilia* remain, one quite perfect. The latter is more prolonged posteriorly than in Cuvier's figure of that bone in *Crocodylus biporcatus*. The anterior half is much like that in a large smooth toothed *Holops* from Tinton Falls, N. J., but presents a pit just behind the anterior tuberosity not found in it. There is a separate oval articular face below this tuberosity at the usual pubic articulation. The anterior angle of the crest of the ilium is not prominent; more so in the *Holops* above noted. Crest longitudinally rugose.

	In.	Lin.		Lin.
Length ilium,	6	7	Depth anterior tuberosity,	22.4
Depth behind ischiadic suture,	2	3	Length posterior hook ilium,	32.2
Depth at do	3	5.7		

The *dermal bones* are very characteristic and distinguish the genus. They differ in two points from those of *Thoracosaurus* and *Holops*; first, in having no pits; second, in having a prominent median keel. They are rather small, subquadrate, and with a very thick, always obtuse, and sometimes elevated median carina. The latter has rather the form of a knob. Many of the bones consist chiefly of this knob with a small basis. The superior surface is dotted with a few punctæ and grooves. Length of one of the largest 24.1 lines; depth 5 lines; width 11.5. Those probably of the cervical or anterior dorsal region have been described by me under *Holops obscurus*, p. 78. I believe they should be referred here, as those from the dorsal region of the present specimen approach them very closely. Those referred to the *Bottosaurus*, p. 66, should be assigned elsewhere." Cope's description of the dermal plates in his description of *Holops obscurus* is as follows: "Of *dermal bones*, those of two species, perhaps of more, were procured from the excavations that produced four species of Gavials, with *Bottosaurus*, . . . and to which they are to be referred is not very clear. In the one, the pits or fovea are very large and are separated by narrow elevated partitions; in the other they are small and are separated by flat intervals wider than themselves. In the former the fovea extend to the edges of the plate on the bevelled edges; in the latter, the bevelled edges are without foveæ. Leidy says of those of this type, 'plates coarsely foveated.' The first described belong to the median series of the present species, as they usually accompany its bones when they occur alone; and the latter to the external series.

Parallelogrammic dermal bones without pits, and with very high longitudinal crests, standing on more than half the length, frequently accompany remains of this species. They are cervical or nuchal bones, and are of relatively large size, equalling those of the dorsal region. The crests are oblique in the direction of their length. Such bones belong to this species, perhaps to *H. cordatus* also." This latter description does not, evidently, refer to the type material, but to referred material.

The species may provisionally be considered valid.

***Bottosaurus perrugosus* Cope**

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1874, 'Review of the Vertebrata of the Cretaceous Period found West of the Mississippi River,' Bull. U. S. Geol. and Geog. Surv. Terr., F. V. Hayden in Charge, I, No. 2, first series, pp. 7, 26, 27; also 1874, Rept. U. S. Geol. and Geog. Surv. Terr., F. V. Hayden in Charge, for 1873, pp. 452, 453; also 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, pp. 68, 69, 253, Pl. VI, figs. 5-8.

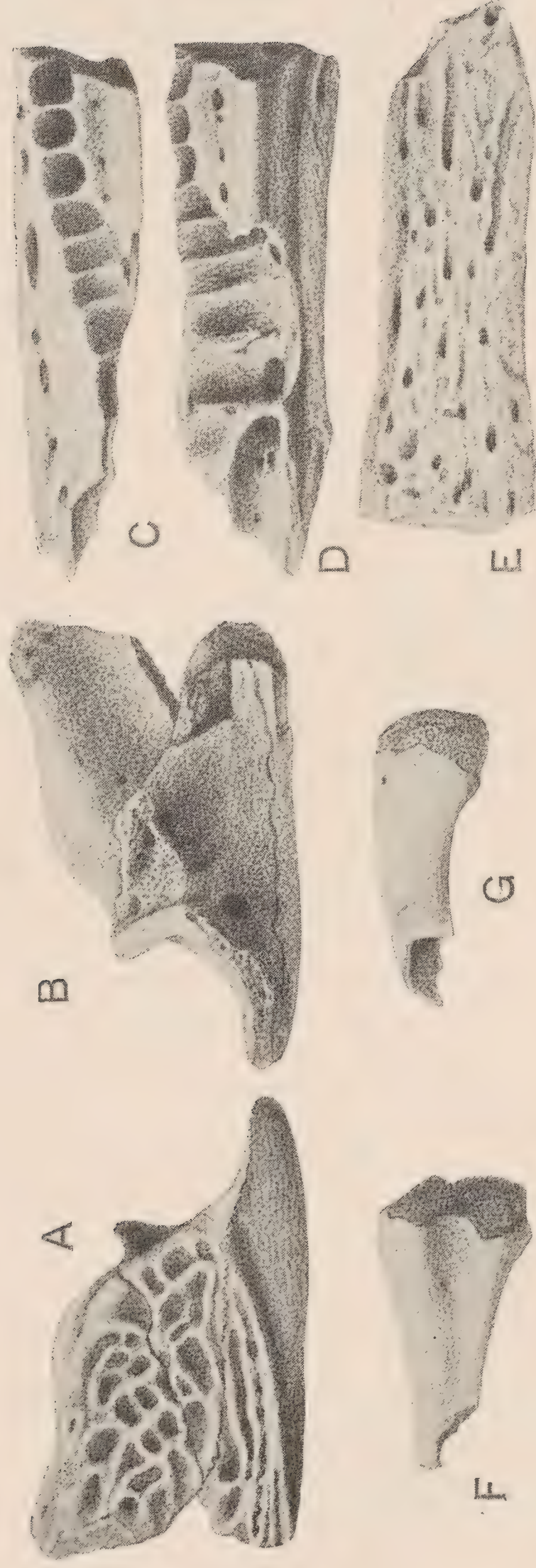


Fig. 11. *Bottosaurus perrugosus* Cope. Type specimen, jaw fragments and femur.

One-half natural size. A, posterior portion of left mandibular ramus, external view; B, the same, internal view; C, portion of dentary bone, superior view; D, the same, internal view; E, distal end of femur, anterior view; F, the same, lateral view. Original type figures. (After Cope.)

SUBSEQUENT REFERENCES.—TOULA, J., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354. LAMBE, L. M., 1899, 'On Reptilian Remains from the Cretaceous of North-Western Canada,' Ottawa Nat., XIII, p. 69. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 514. HATCHER, J. B., 1905, 'Vertebrata' (Judith River Beds), Bull. U. S. Geol. Surv., No. 257, p. 82. LAMBE, L. M., 1907, 'On a New Crocodilian Genus and Species from the Judith River Formation of Alberta,' Trans. Roy. Soc. Canada, Ser. 3, I, pp. 219, 220. GILMORE, C. W., 1911, 'A New Fossil Alligator from the Hell Creek Beds of Montana,' Proc. U. S. Nat. Mus., XLI, p. 298 (Pub. No. 1860), (*Brachychampsia perrugosa*).

ORIGINAL TYPE FIGURES.—COPE, E. D., 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, Pl. VI, figs. 5-8.

TYPE.—Numerous fragments, with vertebræ and portions of the skull.

TYPE LOCALITY AND LEVEL.—Eastern Colorado, upper Cretaceous, probably Laramie beds.

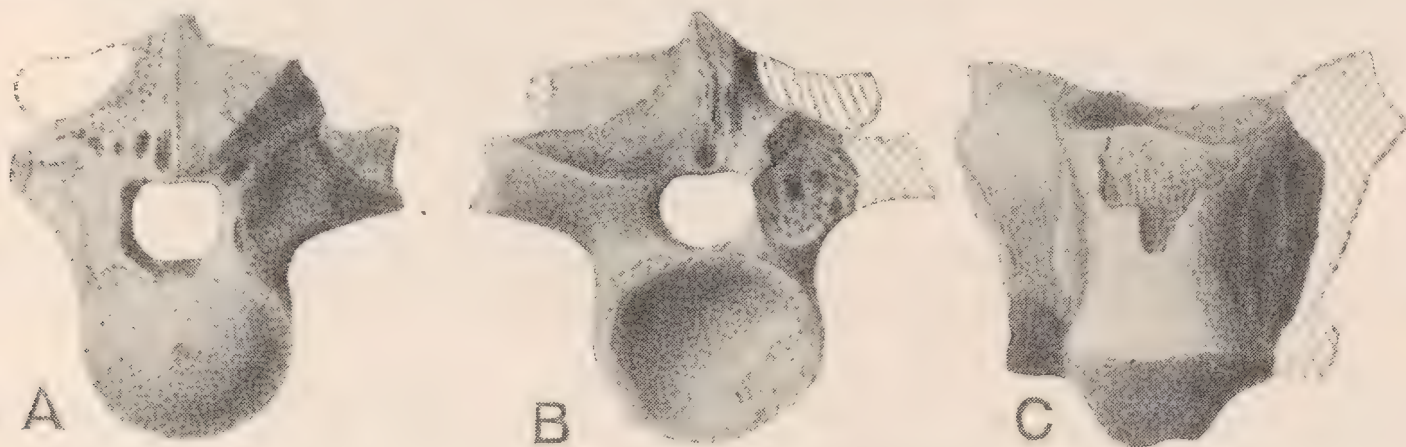


Fig. 12. *Bottosaurus perrugosus* Cope. Type specimen, posterior dorsal vertebra.

One-half natural size. A, posterior view; B, anterior view; C, inferior view. Original type figures.—(After Cope.)

ORIGINAL TYPE DESCRIPTION.—“A portion of the left dentary bone containing alveoli for ten teeth shows that this species is not a gavial. The dental series passes in a curve from the inner to the outer sides of the bones, one or two alveoli behind being probably bounded on the inner side by the splenial only, as in *B. macrorhynchus*, when that bone is in place. The dentary is compressed at this point; in front it is depressed. There is a slight difference in the sizes of the alveoli, but not such as is usual in Tertiary crocodiles. The external face of the bone exhibits deep pits in longitudinal lines. The angle of the mandible is depressed; the cotylus of articulation is partially concealed on the outer side of the elevation of the surangular, whose upper border is parallel with the inferior margin of the ramus for two inches to where it is broken off. The outer face of this region marked by irregular coarse ridges more or less inosculating, separated by deep pits. The lower posterior half of the angular bone is smooth.

A posterior dorsal or lumbar vertebra has a depressed cordate articular cup. The zygapophyses are large and widely spread and strengthened by obtuse ridges running from the base of the neural spine to the posterior margin of the anterior and the posterior outer angle of the posterior. One pit at basis of neural spine in front; two before. Ball prominent; sides of centrum concave.

Measurements.

	M.
Length of fragment of ramus.....	.100
Width in front.....	.034
Depth behind.....	.032
Length of eight alveoli.....	.069
Diameter of largest alveolus.....	.012
Diameter of smallest.....	.007
Width of base of angle of ramus.....	.048
Depth at surangular.....	.034
Length of centrum of vertebra.....	.045
Width of articular cup.....	.031
Vertical diameter of cup.....	.025
Vertical diameter of neural arch.....	.011
Expanse of anterior zygapophyses.....	.056

The specimen is adult, and indicates an animal about the size of the alligator of the Southern States. Its reference to the present genus is provisional only."

The species may provisionally be considered valid.

SPHENOSAURUS Agassiz

ORIGINAL TYPE REFERENCE.—AGASSIZ, L., 1849, [Remarks on the Crocodiles of the Greensand of New Jersey and on *Atlantochelys*], Proc. Acad. Nat. Sci. Phila., IV, p. 169.

SUBSEQUENT REFERENCES.—HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515.

TYPE.—*Crocodylus (Gavialis) clavirostris* Morton.

ORIGINAL TYPE DESCRIPTION.—"Professor Agassiz made some observations upon the *Crocodylus clavirostris* of Morton, and characterized it as a distinct genus under the proposed name of *Sphenosaurus*." (Minutes of meeting of the Academy of Natural Sciences of Philadelphia for March 13, 1849.)

The genus may provisionally be considered synonymous with *Botto-saurus* Agassiz.

Sphenosaurus clavirostris (Morton)

ORIGINAL TYPE REFERENCE.—MORTON, S. G., 1844, 'Description of the Head of a Fossil Crocodile from the Cretaceous Strata of New Jersey,' Proc. Acad. Nat. Sci. Phila., II, pp. 82-85, ((*Crocodylus (Gavialis) clavirostris*)).

SUBSEQUENT REFERENCES.—MORTON, S. G., 1845, 'Description of the Head of a Fossil Crocodile from the Cretaceous Strata of New Jersey,' Amer. Journ. Sci. and Arts, Ser. 2, XLVIII, pp. 265-267, ((*Crocodylus (Gavialis?) clavirostris*. Almost identical with the above)). GIEBEL, C. G., 1847, 'Fauna der Vorwelt,' I, p. 122, (*Cr. clavirostris*). AGASSIZ, L., 1849, [Remarks on the Crocodiles of the Greensand of New Jersey and on *Atlantochelys*], Proc. Acad. Nat. Sci. Phila., IV, p. 169. GIBBES, R. W., 1851, 'A Memoir on *Mosasaurus* and the three Allied New Genera, *Holcodus*, *Conosaurus*, and *Amphorosteus*,' Smith. Contrib. Knowl., II, p. 11. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärablagerungen von

Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515.

ORIGINAL TYPE FIGURE.—MORTON, S. G., 1844, 'Description of the Head of a Fossil Crocodile from the Cretaceous Strata of New Jersey,' Proc. Acad. Nat. Sci. Phila., II, p. 83.

TYPE.—Skull.

TYPE LOCALITY AND LEVEL.—"This remarkably large and admirably preserved relic was found in the cretaceous limestone which overlies the ferruginous marl near Vincentown, in New Jersey."

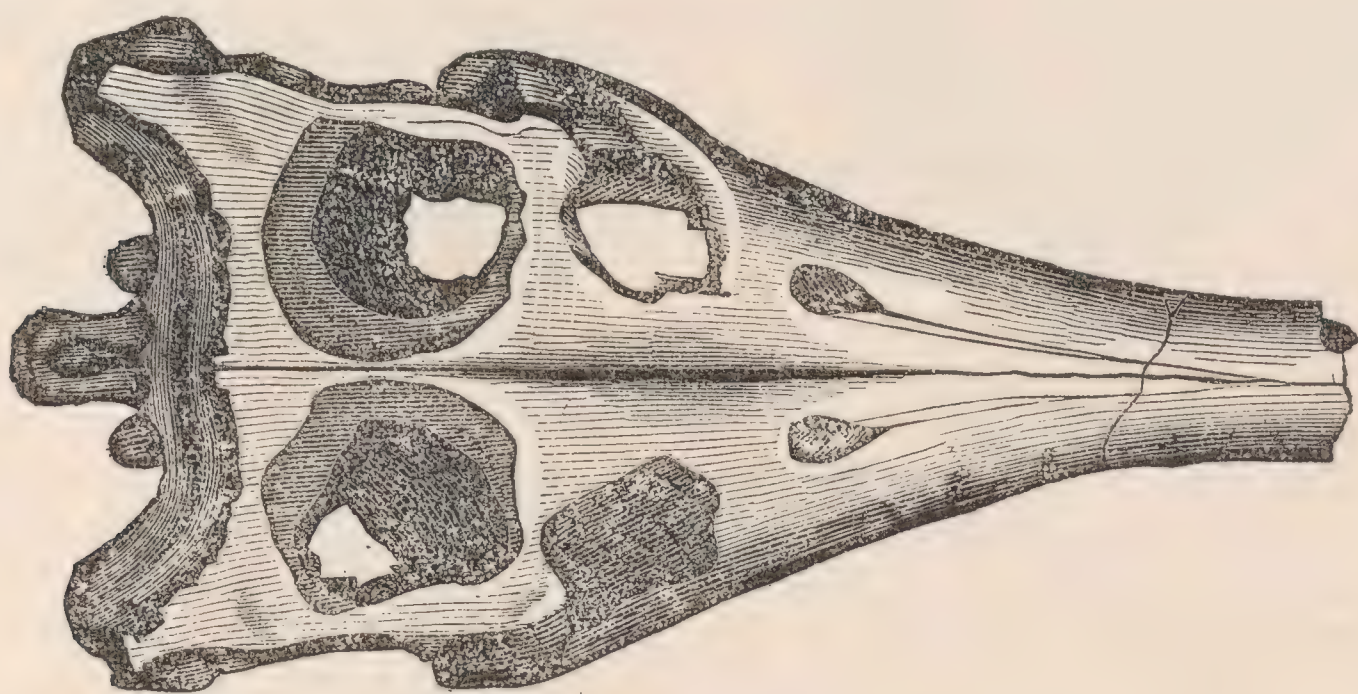


Fig. 13. *Sphenosaurus clavirostris* Morton. Type specimen, skull.

Between one-seventh and one-eighth natural size. Superior view. Original type figure. (After Morton.)

ORIGINAL TYPE DESCRIPTION.—"Skull very broad posteriorly, whence it tapers in a gradual and triangular manner to a narrow, elongated snout. Orbits very large, oblique, and with but slight marginal elevation. Temporal fossæ of great size, and the spiracles? placed immediately below and before the inner margin of the orbit. Length of the head from the superior margin of the occiput to the broken end of the snout 23 inches: width of the occiput behind, $12\frac{1}{2}$ inches; lateral diameter of orbit $3\frac{1}{2}$ inches; lateral diameter of temporal fossæ $4\frac{1}{2}$ inches. Remaining teeth 13 on each side. Lateral diameter of terminal end of the snout $3\frac{1}{4}$ inches.

This species is wholly unlike any other, fossil or recent, with which I have been able to compare it. It seems to form an intermediate link between the Gavials and true Crocodiles, for the snout, though long and narrow, is gradually and not abruptly produced from the head, and has probably been from eight to twelve inches longer than it now is."

Provisionally considered synonymous with *Thoracosaurus neocesaricensis* De Kay.

HYPOSAURUS Owen

ORIGINAL TYPE REFERENCE.—OWEN, R., 1849, 'Notes on Remains of Fossil Reptiles discovered by Prof. Henry Rogers of Pennsylvania, U. S., in Greensand Formations of New Jersey,' Quart. Journ. Geol. Soc. London, V, p. 383.

SUBSEQUENT REFERENCES.—GIBBES, R. W., 1851, 'A Memoir on *Mosasaurus*, and the three Allied New Genera, *Holcodus*, *Conosaurus*, and *Amphorosteus*,' Smith. Contrib. Knowl., II, Art. 5, p. 13. COPE, E. D., 1866, 'On the Structure and Distribution of Arciferous Anura,' Journ. Acad. Nat. Sci. Phila., Ser. 2, IV, p. 111; 1869, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N.S., XIV, Part 1, Art. 1, p. 80; 1875, 'On Green-Sand Vertebrata,' Proc. Acad. Nat. Sci. Phila., XXVII, p. 19. MARSH, O. C., 1877, 'Introduction and Succession of Vertebrate Life in America,' Amer. Journ. Sci. and Arts., Ser. 3, XIV, Art. 42, p. 347. LYDEKKER, R., 1888, 'Catalogue of the Fossil Reptilia and Amphibia in the British Museum,' Part 1, p. 90. NICHOLSON, H. A., AND LYDEKKER, R., 1889, 'A Manual of Palæontology for the Use of Students with a General Introduction on the Principles of Palæontology,' p. 1190. ZITTEL, K. VON, 1890, 'Handbuch der Palæontologie,' Abth. 1, Palæozoologie, III, Vertebrata, pp. 672, 676. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 516. WILLISTON, S. W., 1906, 'American Amphicælian Crocodiles,' Journ. Geol., XIV, pp. 1-7. BERRY, E. W., 1916, 'Vertebrata,' Maryland Geol. Surv., Upper Cretaceous, p. 349.

TYPE.—*Hyposaurus rogersii* Owen.

ORIGINAL TYPE DESCRIPTION.—"The degree of concavity of the two articular extremities of the centrum corresponds with that in the *Teleosauroids*, to which family of amphicælian *Crocodylia* these vertebræ are referable. They indicate, however, a particular genus in that family, of which, from their stratum, it would seem to be the latest representative; and I propose the name *Hyposaurus* for this genus, in reference to the characteristic process—the hypapophysis, and suggest that the species, when its characters are more fully worked out, should be called after the distinguished and amiable geologist to whom we are indebted for our knowledge of the existence of such a *Teleosauroid* in the cretaceous æra."

The genus may provisionally be considered as synonymous with *Goniopholis* Owen.

***Hyposaurus rogersii* Owen**

ORIGINAL TYPE REFERENCE.—OWEN, R., 1849, 'Notes on Remains of Fossil Reptiles discovered by Prof. Henry Rogers of Pennsylvania, U. S., in Greensand Formations of New Jersey,' Quart. Journ. Geol. Soc. London, V, p. 383, Pl. XI, figs. 7-10.

SUBSEQUENT REFERENCES.—GIBBES, R. W., 1851, 'A Memoir on *Mosasaurus* and the three Allied New Genera, *Holcodus*, *Conosaurus*, and *Amphorosteus*,' Smith. Contrib. Knowl., II, Art. 5, p. 9, Pl. III, figs. 6, 7, 8, 13, (*Holcodus acutidens*). LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, pp. 18-21, 116, Pl. III, figs. 4, 16-21; Pl. IV, figs. 1-12; 1872 (date on title-page), 'Brief Review of a Memoir on the Cretaceous Reptiles of the United States, Published in the Fourteenth Volume of the Smithsonian Contributions to Knowledge,' Ann. Rept. Board of Regents Smith. Inst. for 1864 (1865 according to Hay). COPE, E. D., 1867, 'The Fossil Reptiles of New Jersey,' Amer. Nat., I, p. 26, (*Hyposaurus Rodgersi*); 1869, 'Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,' in 'Geology of New Jersey,' by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736, (*Hyposaurus Rogersi*); 1869, 'Synopsis of the Extinct

Batrachia, Reptilia and Aves of North America,' Trans. Amer. Phil. Soc., N.S., XIV, pp. 80-82, Pl. iv, figs. 10, 11; 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, p. 250. WILLISTON, S. W., 1894, 'On Various Vertebrate Remains from the Lowermost

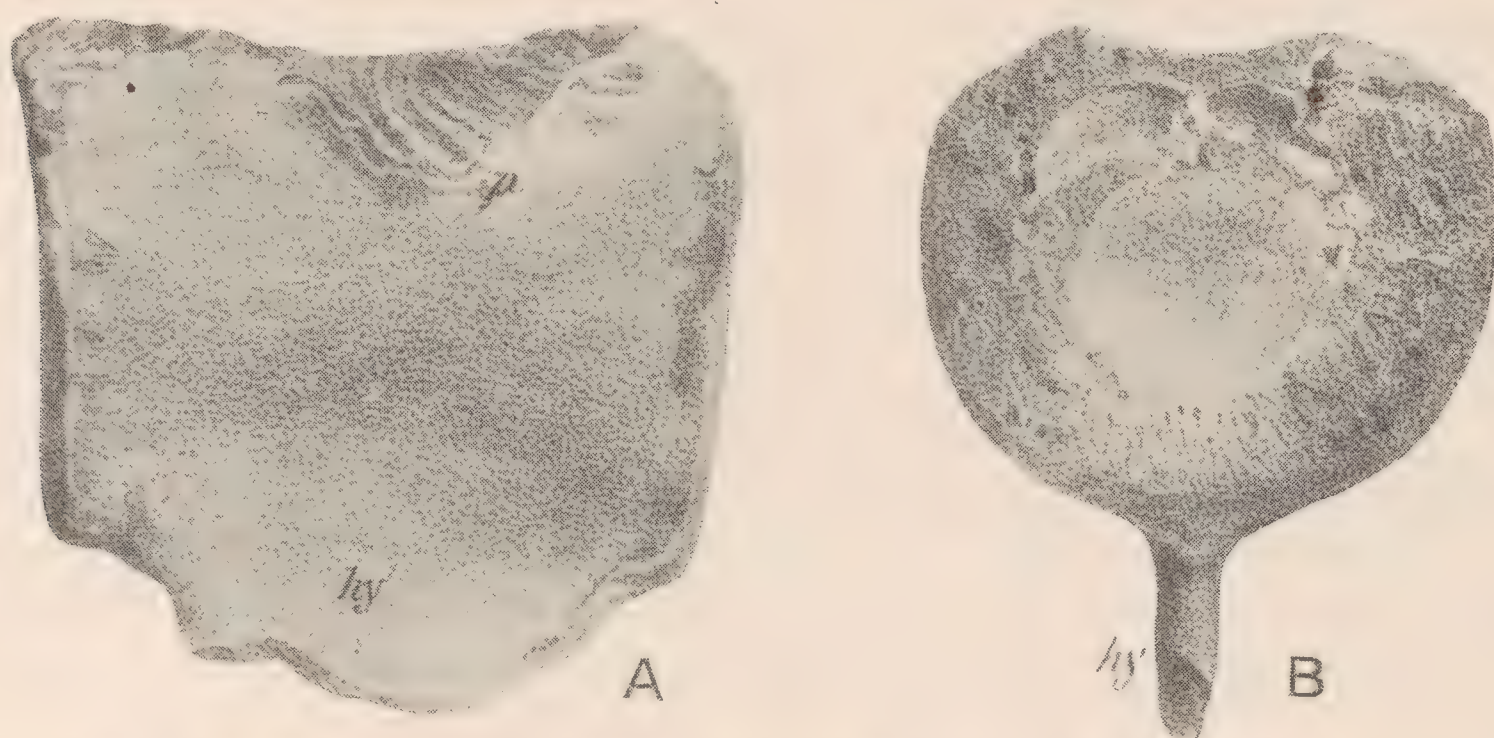


Fig. 14. *Hyposaurus rogersii* Owen. Type specimen, anterior dorsal centrum.

Natural size. A, lateral view, right side; B, inferior view; *hy*, base of hypapophysis; *p*, base of parapophysis. Original type figures. (After Owen.)

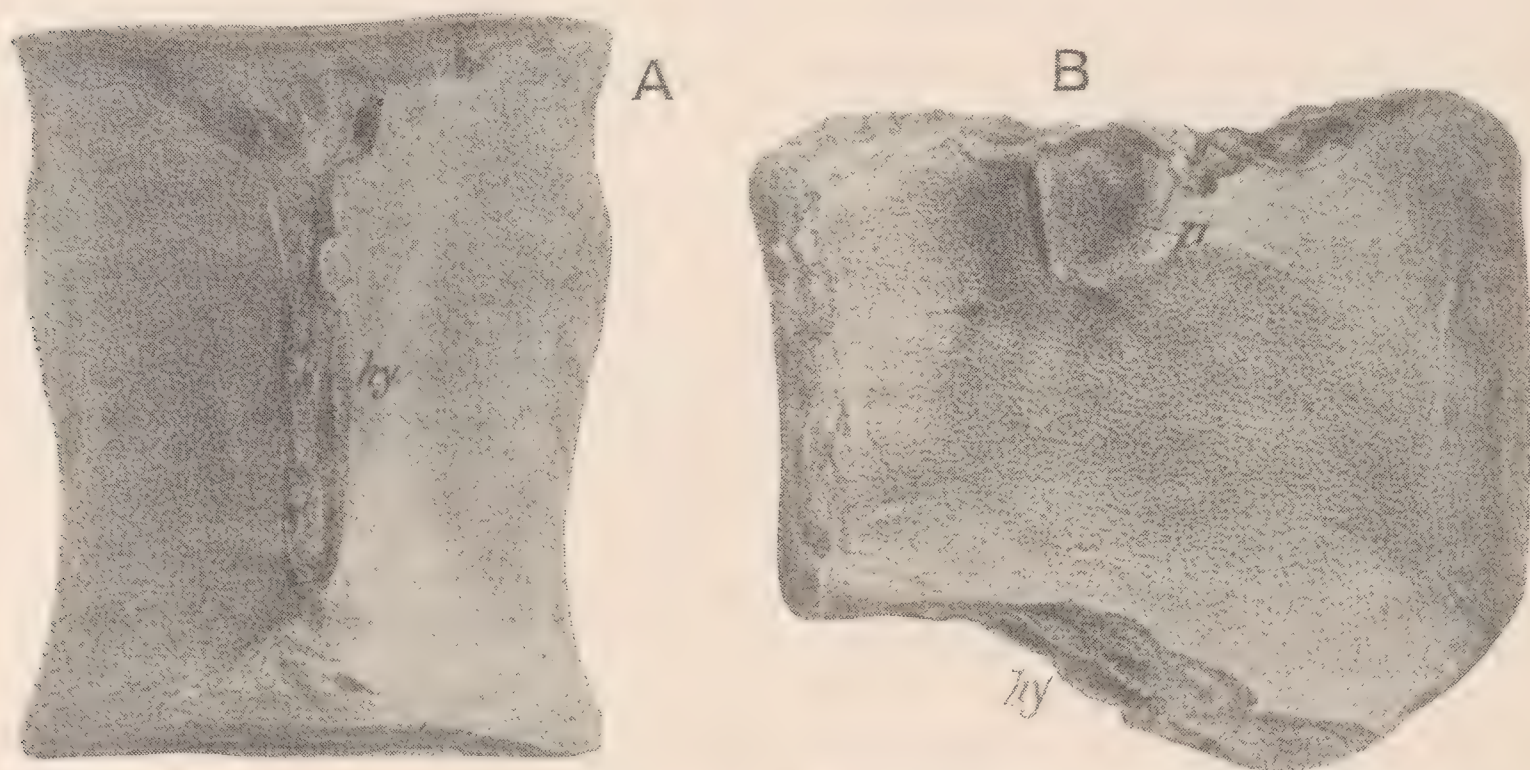


Fig. 15. *Hyposaurus rogersii* Owen. Type specimen, anterior dorsal centrum.

Natural size. A, lateral view, right side; B, posterior view; *hy*, base of hypapophysis; *p*, base of parapophysis. Original type figures. (After Owen.)

Cretaceous of Kansas,' Kans. Univ. Quart., III, p. 4, Pl. i, figs. 4, 5, (*Hyposaurus rodgersi*); 1898, 'Crocodiles,' Kans. Univ. Quart., IV, Part 1, pp. 76-78, figs. 3, 4. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 516. WILLISTON, S. W., 1906, 'American Amphicœlian Crocodiles,' Journ. Geol., XIV, p. 4. BERRY, E. W., 1916, 'Vertebrata,' Maryland Geol. Surv., Upper Cretaceous, p. 349, Pl. VIII, figs. 3, 4.

ORIGINAL TYPE FIGURES.—OWEN, R., 1849, 'Notes on Remains of Fossil Reptiles discovered by Prof. Henry Rogers of Pennsylvania, U. S., in Greensand Formations of New Jersey,' Quart. Journ. Geol. Soc. London, V, Pl. xi, figs. 7-10.

TYPE.—Two anterior dorsal vertebral centra.

TYPE LOCALITY AND LEVEL.—Southern New Jersey. Upper Cretaceous Greensands.

ORIGINAL TYPE DESCRIPTION.—“The peculiar and distinctive character of these vertebræ is shown in the large size, and especially in great antero-posterior extent of the hypapophysis. Its base occupies the whole extent of the median line of the inferior surface between the prominent borders of the anterior and posterior articular ends of the centrum; and the length of this large lamelliform hypapophysis seems to have been considerable, since, in the vertebra, figs, 8, 10, in which upwards of half an inch of its base is retained, there is little diminution of thickness at the fractured base.

The degree of concavity of the two articular extremities of the centrum corresponds with that in the *Teleosauroids*, to which family of amphicælian *Crocodylia* these vertebræ are referable. They indicate, however, a particular genus in that family, of which, from their stratum, it would seem to be the latest representative.”

The species may provisionally be considered valid.

***Hyposaurus fraterculus* Cope**

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1869, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., XIV, N.S., Part 1, p. 82.

SUBSEQUENT REFERENCES.—COPE, E. D., 1869, 'Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,' in 'Geology of New Jersey,' by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736; 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, p. 254, (*Gavialis fraterculus*); 1875, 'On Greensand Vertebrata,' Proc. Acad. Nat. Sci., Phila., XXVII, p. 19. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354, (*Gavialis fraterculus*). HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515. WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol., XIV, p. 1.

ORIGINAL TYPE FIGURE.—No figure of the type has previously been published. The type is figured in this article (Fig. 16).

TYPE.—Portion of a mandibular ramus. Amer. Mus. Cope Coll. No. 2198.

TYPE LOCALITY AND LEVEL.—Birmingham, Burlington County, New Jersey. Middle Greensand beds, Cretaceous.

ORIGINAL TYPE DESCRIPTION.—“This small species seems to be clearly indicated by a portion of the ramus mandibuli containing three and half a fourth alveoli, and two perfect teeth. These parts are less than half the size of those of the smaller individual of *H. rogersi*, whose maxillary bone and teeth are described in the preceding article. The crowns of the teeth are shorter and more compressed than those in the corresponding part of the jaws in *H. rogersi*; they are marked with a coarse obtuse fluting to near the tip, with a finely striate enamel as in *Holops glyptodon*; in those of *H. rogersi*, the enamel is smooth and ridged by fine keels, which do not extend more than half the length of the crown.

That the animal of which I describe this fragment was not the young of the larger *Hyposaurus*, is, I think, indicated by the deep grooving and strong ridging of the dense layer of bone of the ramus; by the minute pulp cavity of the crowns of the teeth, and by the well developed successional tooth in the fang of one of the latter, whose apex has nearly reached the alveolar margin. That the individual is not fully grown is probable, but that it is of smaller species than the *H. rogersi*, there appears to be little room for doubt.

The ramus is scarcely flattened below, as is the case with most gavials, and the depth at the symphysis is equal the width of each ramus. Sculpture in deep longitudinal grooves slightly inosculating. Teeth directed very little outwards: their fangs and crowns are considerably compressed; the antero-posterior cutting edge is stronger than the ridges, and does not diminish to the base of the crown. Viewed from within the form is symmetrical and straight; from behind the crown is greatly incurved. The outline of the crown from within is an isosceles triangle, the width, more than .66 the height. Ribs on the inner face, seven, on the outer, eight. A few teeth in the jaws of *H. rogersi* are as short and broad as those here described, but they are not found in the middle of the series as in this species, but probably belong in the posterior alveoli, as occurs in some alligators.

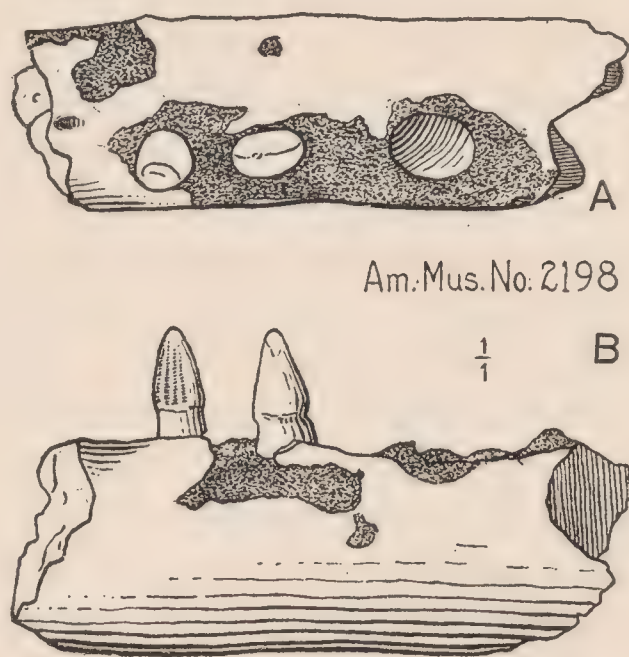


Fig. 16. *Hyposaurus fraterculus* Cope. Type specimen, part of mandibular ramus (Amer. Mus. Cope Coll. No. 2198).
Natural size. A, superior view; B, external view.

	<i>Lines.</i>
Length of fragment,	19.3
Width at middle,	6.
No. of alveolæ in an inch; three and half and interspace.	
Length tooth above alveolus,	4.
“ crown of tooth,	2.75
Width “ “ “ at base,	1.75”

The species may provisionally be considered valid.

Hyposaurus ferox Marsh

ORIGINAL TYPE REFERENCE.—MARSH, O. C., 1871, [Communication on some new Reptiles and Fishes from the Cretaceous and Tertiary], Proc. Acad. Nat. Sci., Phila., XXIII, p. 104.

SUBSEQUENT REFERENCES.—HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 516. WILLISTON, S. W., 1906, ‘American Amphicoelian Crocodiles,’ Journ. Geol., XIV, p. 4.

ORIGINAL TYPE FIGURE.—No figure of the type has been published.

TYPE.—Two teeth, Yale Mus.

TYPE LOCALITY AND LEVEL.—Birmingham, New Jersey. Middle marl bed of the Cretaceous Greensands.

ORIGINAL TYPE DESCRIPTION.—“Professor Marsh, of Yale College, made a communication on some new reptiles and fishes from the Cretaceous and Tertiary formations. . . . Another new Cretaceous reptile was indicated by two teeth, which were found together in the middle marl bed at Birmingham, New Jersey. They apparently belonged to a Crocodilian, probably allied to *Hyposaurus*. One of the teeth, apparently from the anterior part of the jaw, is long, pointed, nearly round, and covered with strong angular but smooth ridges, except just at the apex, where they disappear. The posterior cutting edge is sharp and prominent, and extends the entire length of the crown. The anterior edge is only distinct a short distance near the apex. The second tooth has the crown short and compressed, with irregular ridges, and resembles somewhat the posterior teeth of *Hyposaurus*. These specimens indicate a species considerably larger than *H. Rogersii*, which, until its generic characters are more fully determined, may be called *Hyposaurus ferox*.” (Records of meeting of the Academy of Natural Sciences of Philadelphia).

The species may provisionally be considered valid.

THORACOSAURUS Leidy

ORIGINAL TYPE REFERENCE.—LEIDY, J., 1852, [Descriptions of *Delphinus conradi* and *Thoracosaurus grandis*], Proc. Acad. Nat. Sci. Phila., VI, p. 35.

SUBSEQUENT REFERENCES.—LEIDY, J., 1865, ‘Cretaceous Reptiles of the United States,’ Smith. Contrib. Knowl., XIV, p. 5. COPE, E. D., 1869, ‘Synopsis of the Extinct Batrachia and Reptilia of North America,’ Trans. Amer. Phil. Soc., N.S., XIV, Part 1, Art. 1, p. 79. MARSH, O. C., 1877, ‘Introduction and Succession of Vertebrate Life in America,’ Amer. Journ. Sci. and Arts, Ser. 3, XIV, Art. 42, p. 346. TOULA, F., AND KAIL, J. A., 1885, ‘Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,’ Denkschr. k. Akad. Wissensch. Wien, p. 354. LYDEKKER, R., 1886, ‘Siwalik Crocodilia, Lacertilia, and Ophidia,’ Mem. Geol. Surv. India, Palæontologia Indica, Ser. 10, III, Part 7, pp. 3 (211), 12 (220), 27 (235). LUCAS, F. A., 1898, ‘Contributions to Paleontology. 1. A New Crocodile from the Trias of Southern Utah,’ Amer. Journ. Sci., Ser. 4, VI, p. 399. COPE, E. D., 1900, ‘The Crocodilians, Lizards and Snakes of North America,’ Rept. U. S. Nat. Mus. for 1898, p. 161. HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 515. ANDREWS, C. W., 1906, ‘A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt,’ p. 269, Brit. Mus. WILLISTON, S. W., 1906, ‘American Amphicoelian Crocodiles,’ Journ. Geol., XIV, pp. 2, 17; 1914, ‘Water Reptiles of the Past and Present,’ p. 207. SELLARDS, E. H., 1915, ‘A New Gavial from the Late Tertiary of Florida,’ Amer. Journ. Sci., Ser. 4, XL, p. 137. BERRY, E. W., 1916, ‘Vertebrata,’ Maryland Geol. Surv., Upper Cretaceous, pp. 347, 348, Pl. VIII, fig. 11.

TYPE.—*Thoracosaurus grandis* Leidy = *Gavialis neocesariensis* De Kay.

ORIGINAL TYPE DESCRIPTION.—The characters of the genus were not separated from those of the type species by Leidy. See *Thoracosaurus grandis*.

The genus may provisionally be considered valid.

Thoracosaurus neocesariensis (De Kay)

ORIGINAL TYPE REFERENCES.—DE KAY, J. E., 1833 (according to Hay), ‘Observations on a Fossil Jaw of a Species of Gavial, from West Jersey,’ Ann. Lyc. Nat.

Hist. N. Y., III, 1827–1833, pp. 156–165, Pl. III, figs. 7–11, (“Gavial,” with no specific designation). DE KAY, J. E., 1842, ‘Zoology of New York,’ Part 3, Reptiles and Amphibia, p. 28, Pl. XXII, fig. 59, (*Gavialis neocesariensis*).

SUBSEQUENT REFERENCES.—MORTON, S. G., 1844, ‘Description of the Head of a Fossil Crocodile from the Cretaceous Strata of New Jersey,’ Proc. Acad. Nat. Sci. Phila., II, pp. 82–85, 1 fig, ((*Crocodylus* (*Gavialis*?) *clavirostris*. This is described as a new species. Hay treats it as a synonym of *T. neocesariensis*)). MORTON, S. G., 1845, ‘Description of the Head of a Fossil Crocodile from the Cretaceous Strata of New Jersey,’ Amer. Journ. Sci. and Arts, XLVIII, pp. 265–267, 1 fig, (identical, with the exception of the spelling of a word, with the preceding). GIEBEL, C. G., 1847, ‘Fauna der Vorwelt,’ p. 122, (*Crocodylus clavirostris*, referring to Morton’s species). AGASSIZ, L., 1849, [Remarks on the Crocodiles of the Greensand of New Jersey and on *Atlantochelys*], Proc. Acad. Nat. Sci. Phila., IV, p. 169, (*Sphenosaurus clavirostris* for Morton’s *Crocodylus clavirostris*). OWEN, R., 1849, ‘Notes on Remains of Fossil Reptiles Discovered by Prof. Henry Rogers of Pennsylvania, U. S., in Greensand Formations of New Jersey,’ Quart. Journ. Geol. Soc. London, V, p. 381, Pl. x, figs. 1, 2, (*Crocodylus basifissus* considered by Hay equivalent to *T. neocesariensis*). GIBBES, R. W., 1851, ‘Memoir on Mosasaurus and the three Allied New Genera, *Holcodus*, *Conosaurus*, and *Amphorosteus*,’ Smith. Contrib. Knowl., II, pp. 7, 13, (*Sphenosaurus clavirostris* and *Crocodylus basifissus*). LEIDY, J., 1852, [Descriptions of *Delphinus conradi* and *Thoracosaurus grandis*], Proc. Acad. Nat. Sci. Phila., VI, p. 35, (*Thoracosaurus grandis* treated by Hay as a synonym of *T. neocesariensis*); 1852, ‘Description of a new Species of Crocodile from the Miocene of Virginia,’ Journ. Acad. Nat. Sci. Phila., Second Series, II, pp. 135, 136, (*Crocodylus Dekayi* proposed for *T. neocesariensis* De Kay. *Sphenosaurus clavirostris*). OWEN, R., 1860, ‘On the Orders of Fossil and Recent Reptilia, and their Distribution in Time,’ Rept. Brit. Assoc. Adv. Sci. for 1859, p. 165, (*Crocodylus basifissus*). LEIDY, J., 1865, ‘Cretaceous Reptiles of the United States,’ Smith. Contrib. Knowl., XIV, Art. 6, pp. 5–12, 115, Pl. I, figs. 1–6; Pl. II, figs. 1–3; Pl. III, figs. 5–11; 1865, ‘Brief Review of a Memoir on the Cretaceous Reptiles of the United States, published in the Fourteenth Volume of the Smithsonian Contributions to Knowledge,’ Ann. Rept. Board of Regents Smith. Inst. for 1864, p. 67. COPE, E. D., 1867, ‘The Fossil Reptiles of New Jersey,’ Amer. Nat., I, p. 26. (*T. neocæsariensis*); 1869, ‘Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,’ in ‘Geology of New Jersey,’ by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736, (*T. neocæsariensis*); 1869, ‘Synopsis of the Extinct Batrachia and Reptilia of North America,’ Trans. Amer. Phil. Soc., N.S., XIV, Part 1, pp. 68, 79, 80, (*T. neocæsariensis*); 1875, ‘The Vertebrata of the Cretaceous Formations of the West,’ Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, p. 250, (*T. neocæsariensis*); TOULA, F., AND KAIL, J. A., 1885, ‘Über einen Krokodil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich,’ Denkschr. k. Akad. Wissensch. Wien, p. 354. KOKEN, E., 1888, ‘Thoracosaurus macrorhynchus Bl. aus der Tuffkreide von Maastricht,’ Zeitschr. d. Deutsch. Geol. Gesellsch. (Jahrg. 1888), pp. 754–773, (*T. neocæsariensis*). WOODWARD, A. SMITH, 1890, ‘Vertebrate Palæontology in some American and Canadian Museums,’ Geol. Mag., N.S., Dec. 3, VII, p. 393, (*T. neocæsariensis*). ZITTEL, K. VON, 1890, ‘Handbuch der Palæontologie,’ Abth. 1, Palæozoologie, III, Vertebrata, p. 673. HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 515. WILLISTON, S. W., 1906, ‘American Amphicoelian Crocodiles,’ Journ.

Geol., XIV, p. 2. ANDREWS, C. W., 1906, 'A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt,' p. 269, Brit. Mus. BERRY, E. W., 1916, 'Vertebrata,' Maryland Geol. Surv., Upper Cretaceous, pp. 347, 348, Pl. VIII, figs. 1, 2.

ORIGINAL TYPE FIGURES.—DE KAY., J. E., 1833 (according to Hay), 'Observations on a Fossil Jaw of a Species of Gavial, from West Jersey,' Ann. Lyc. Nat. Hist., N. Y., III, 1827-1836, pp. 156-165, Pl. III, figs. 7-10.

TYPE.—Fragments of the jaw.

TYPE LOCALITY AND LEVEL.—Southern part of New Jersey. Upper Cretaceous Greensands.



Fig. 17. *Thoracosaurus neocesariensis* De Kay. Type specimen, jaw fragments.

About one-third natural size. A, portion of left dentary, oblique view; B, portion of right dentary, oblique view; C, portions of dentary and splenial bones, superior view; D, immature tooth. Original type figures. (After De Kay.)

ORIGINAL TYPE DESCRIPTION.—“*Dimensions of Fragment, . . of left Dental Bone.*

Length 4.1 Extreme breadth 1.5 nearly.

Distance between sockets .8.

Depth of sockets 1.5.

Projection of tooth above the alveole 1.1.

Transverse diam. of tooth above the socket .5.

Longitud. diam. .6.

Diameter within the socket .65.

In order to understand the structure and arrangement of these teeth, it may be necessary to recur to the process of dentition, as it exists among these animals. Their number never varies with age; and although they are formed by superimposed coats, yet their interior is always hollow. At the bottom of the socket is to be found the replacing tooth, which gradually increasing, ascends into the hollow of the old tooth, presses upon, and of course destroys, the pulpy nucleus within, which has furnished nutriment to the old tooth. This latter tooth, of course, easily falls out, is replaced by the new one, which, in its turn, makes way for another; and this is often

repeated during the whole life-time of the animal. Hence, at any period, if we examine the teeth of these animals we shall find always the replacing tooth either within the old one or in a rudimentary form, or at the bottom of the socket. Among the loose fragments, to which I regret being unable to assign its proper place, but which is near the bottom of a socket, is a small replacing tooth, .25 in length. It is of a conical form, and blunt at its summit. . . It is worthy of remark, that this tooth, instead of originating from the centre of the bottom of the socket, lies near the inferior and anterior side. Are we authorized to infer, that the individual species under examination belonged not to an adult animal, but to one which had not yet attained its full growth, and that the position of this replacing tooth indicates that the outer edge of the alveole would be advanced farther with the growth of the animal? According to Cuvier, the replacing tooth generally commences near the inner surface; and hence it is on this side, by its compression, that the old tooth frequently exhibits, near the upper edge of the alveole, a notch or indentation on its inner side, proving that absorption has taken place.

The sockets and parts of sockets are .8 apart on the superior surface of this dental bone, and approach nearer at their bases. The central socket contains the most perfect tooth in all the fragments. Fig. 7 [Fig. 17A of this work] represents its appearance, describing a segment of a circle whose diameter is four inches. The whole length of the tooth is 2.6. The direction of this curve is forward and outwardly; or, in other words, its lower extremity is near the internal plane of the dental bone, while the external portion of the tooth is not far from the outer edge of the same bone. Within the socket the tooth is cylindrical, and, as is common among animals of this class, it is larger than the exposed portion. It is hollow, and filled with the soil in which it was found. The upper part of the tooth is much injured, but enough remains to enable us to describe its general form, which is conical, recurved, and rather broader in the transverse axis of its base than in the longitudinal direction of the dental bone. A very minute portion is all that is left of its external coat; but from this we may state, that it is of a brown colour, very minutely striated, and, in a proper light, appears divided into a number of minute facets. We cannot, however, from this small fragment, aver that the same appearance pervades the whole crown of the tooth; nor can we pronounce with certainty that the teeth were furnished with edges.

. . . *right Dental Bone.*

This fragment, in fact, consists of portions of three bones; but in the figure, the right dental bone only is shown, in order to exhibit the figure and direction of the sockets. Its principal dimensions are as follows:—

Total length 5.7.

Breadth undetermined, on account of the imperfection of the fragment.

Depth at symphysis 2.1.

Depth, just anterior to the second tooth, 1.7.

Depth of socket behind, 1.6.

Depth of jaw at anterior portion 1.6.

Distance between first and second alveole .9.

 between 2d and 3d .7.

 between 3d and 4th .4.

Of the fourth, or posterior socket, only a portion remains.—The third is filled up with the body of a tooth, which is visible in its whole length, and exhibits its base

compressed in the direction of the vertical plane of the jaw. The second and first alveoles are likewise filled with the body of teeth, but are concealed in consequence of the perfect state of the bone in these places. At the anterior part of this bone is a portion of another socket, which cannot be exhibited in the figure. Connected with the dental bone are two others, which will be better understood when we connect these fragments in their original position. We shall then have fig. 10,—[Fig. 17C of this work] a large and important portion of the lower jaw of a fossil reptile.

In this figure *a* represents the fragments of the left, and *b* of the right dental bones already described, as seen from above.

At *c c* are seen portions of two bones which are peculiar to animals of this family, and were termed, by Adrian Camper, opercular bones: they form the symphysis of the lower jaw, and the dental bones repose against them, and go off posteriorly to form the branches of the lower maxillary.

The total length of the fragment of the opercular bone of the right side is 7.8.

From the symphysis to the anterior termination of the same bone is 6.2.

Breadth of both operculars, just before the symphysis, is 2.4.

Presumed breadth at symphysis 4.

Breadth of jaw, at outer extremity 2.7.

Thickness at same place 1.7.

The upper surface of the opercular bones is smooth, and its substance is very compact. The surface of the right dental bone is likewise tolerably even; but its side, and particularly its inferior surface, has the same corroded and worm-eaten appearance noticed in its companion on the left side.

We are now furnished with sufficient data to pronounce that the fragments under consideration are a portion of the lower jaw of some species of animal belonging to a family of reptiles which includes the crocodiles." (De Kay, 1833.)

(De Kay, 1842) "With from fifteen to eighteen distant, conical teeth. Length 9-10 feet."

The species may provisionally be considered valid.

Thoracosaurus (Crocodilus) basifissus (Owen)

ORIGINAL TYPE REFERENCE.—OWEN, R., 1849, 'Notes on Remains of Fossil Reptiles Discovered by Prof. Henry Rogers of Pennsylvania, U. S., in Greensand Formations of New Jersey,' Quart. Journ. Geol. Soc. London, V, pp. 380, 381, Pl. x, figs. 1, 2, (*Crocodilus basifissus*).

SUBSEQUENT REFERENCES.—LEIDY, J., 1852, 'Description of a new Species of Crocodile from the Miocene of Virginia,' Journ. Acad. Nat. Sci. Phila., II, Ser. 2, p. 135, (*Crocodilus basifissus*). OWEN, R., 1860, 'On the Orders of Fossil and Recent Reptilia, and their Distribution in Time,' Rept. Brit. Assoc. Adv. Sci., Meeting at Aberdeen, 1859, p. 165, (*Crocodilus basifissus*). TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354, (*Alligator basifissus*). HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515. WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol., XIV, p. 2, (*Crocodilus basifissus*).

ORIGINAL TYPE FIGURES.—OWEN, R., 1849, 'Notes on Remains of Fossil Reptiles Discovered by Prof. Henry Rogers of Pennsylvania, U. S., in Greensand

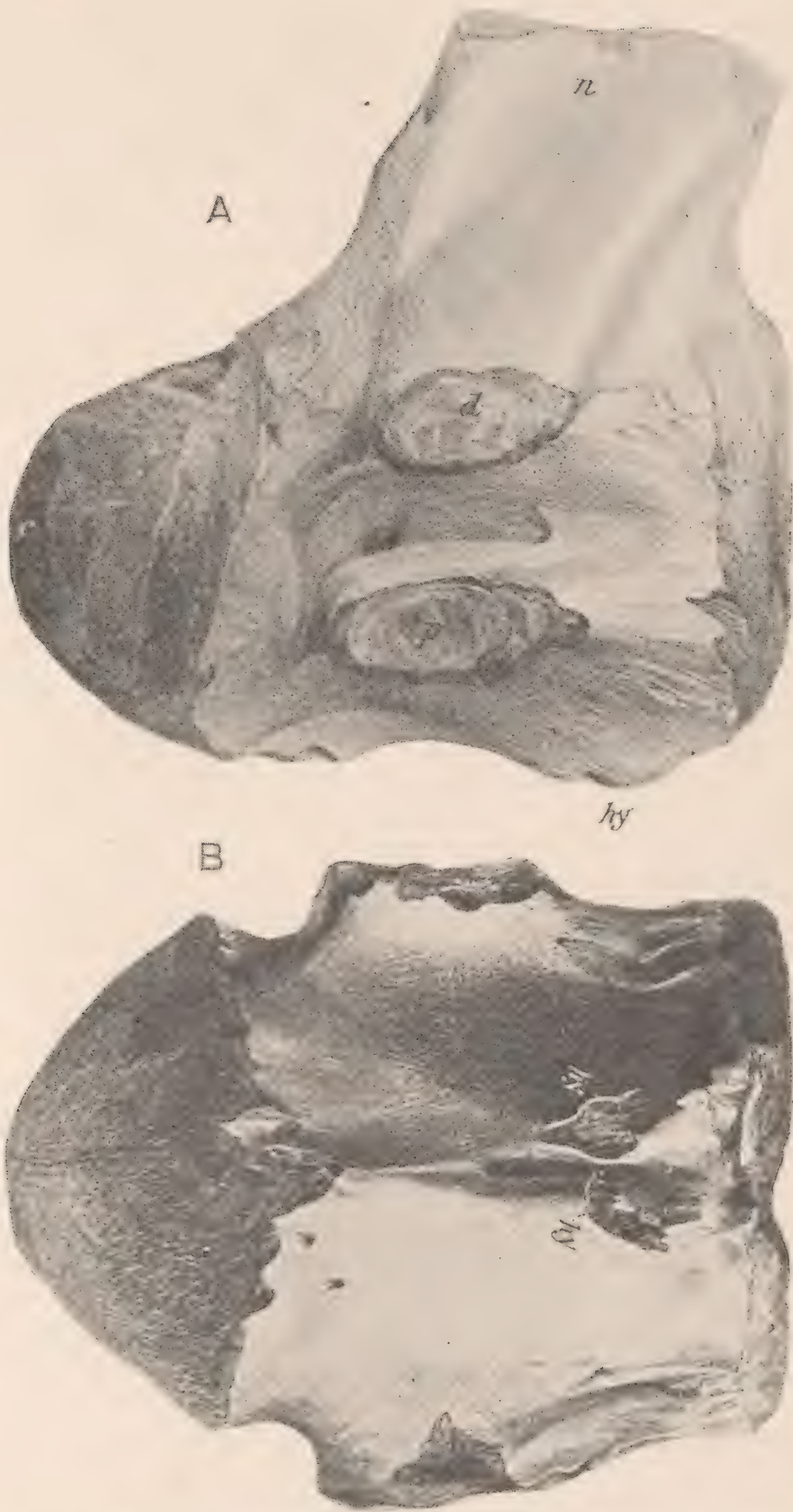


Fig. 18. *Thoracosaurus (Crocodilus) basifissus* (Owen).
Type specimen, cervical vertebra.

Natural size. A, lateral view, right side; B, inferior view; *d*, diapophysis; *hy*, hypapophysis; *n*, neural arch; *p*, parapophysis. Original type figures. (After Owen.)

Formations of New Jersey,' Quart. Journ. Geol. Soc. London, V, pp. 380, 381, Pl. x, figs. 1, 2.

TYPE.—A middle cervical vertebra, fourth or fifth.

TYPE LOCALITY AND LEVEL.—Southern New Jersey. Cretaceous Greensand beds.

ORIGINAL TYPE DESCRIPTION.—“Figures 1 to 4, in Pl. X., are of cervical vertebræ of a Crocodile or Alligator, constructed upon the same (procælian) type as those of the existing species; *i.e.*, having the anterior surface of the body or centrum concave and the posterior one (*c*, figs. 1 & 3) convex.

The numerous vertebræ, cervical, dorsal, lumbar and caudal, of this type, brought over by Prof. Rogers, were divisible into two series; and one of the most characteristic specimens of each of these series is here selected to illustrate the difference, which shows that there were two species of the same genus as the modern Crocodiles or Alligators, which left their remains in the greensand deposits of the United States. The vertebra in question is one of the middle cervical, probably the fourth or fifth, in which the parapophysis (*p*) is still near the lower part of the side of the centrum, the diapophysis (*d*) wholly developed from the base of the neurapophysis (*n*), and in which also a hypapophysis (*hy*) is developed from the under surface of the centrum.

The most marked difference between the vertebræ figs. 1 & 3 is presented by the latter process: in fig. 1 it is double, or divided by a median longitudinal cleft; in fig. 2 it is single, broad, flattened and smooth below. These characters are well and accurately shown in the figs. 2 & 4 of the inferior surface of the vertebræ selected. A corresponding modification of the hypapophysis was presented by other cervical and anterior dorsal vertebræ of each series respectively. But the specific distinction of the two is manifested by other characters. The cervical vertebra, figs. 3 & 4, is longer in proportion to its breadth than figs. 1 & 2; the parapophysis, *p* in fig. 1, comes off from the middle of the side of the centrum: in fig. 3 its origin is more advanced, and extends to the border of the anterior articular cup. And these characters were not those distinguishing different positions of the vertebræ in the cervical series, any more than those of the hypapophyses, but were characteristic of the other cervical vertebræ of each series respectively.

Two species, therefore, of Crocodile or Alligator, were thus established, equalling in size the existing *Alligator lucius* of the Southern States, or the *Crocodylus acutus* of Jamaica.

Neither these, nor any other existing Crocodile of which I have had the opportunity of examining and comparing the vertebræ, presents the same characters of the hypapophyses which have been described and figured in the above fossil vertebræ. I regard the species, therefore, to which these vertebræ respectively belonged as extinct, and agreeably with actual knowledge, the oldest of the modern Crocodilian family.

For the species characterized by vertebræ of the type of that depicted in figs. 1 & 2, I propose the name of *Crocodylus basifissus*; for the species with the inferior process single, short and flattened, that of *Crocodylus basitruncatus*:

The proportions of the vertebræ of the *Crocodylus basifissus* resemble those of the vertebræ of the *Alligator*.”

Leidy considered this form as possibly belonging to the species which he named *Crocodylus dekayi*, but which had already been named

Gavialis neocesariensis by De Kay. Hay considered it as synonymous with the latter. The characters noted by Owen, however, appear to be of specific value, and provisionally, at least, the species may be considered valid, and may be referred to *Thoracosaurus*.

Thoracosaurus grandis Leidy

ORIGINAL TYPE REFERENCE.—LEIDY, J., 1852, [Description of *Thoracosaurus grandis*], Proc. Acad. Nat. Sci. Phila., VI, p. 35.

SUBSEQUENT REFERENCES.—HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 515. WILLISTON, S. W., 1906, ‘American Amphicœlian Crocodiles,’ Journ. Geol., XIV, p. 2.

ORIGINAL TYPE FIGURE.—No figure of the type has been published.

TYPE.—A dermal scute and half of another.

TYPE LOCALITY AND LEVEL.—Mount Holly, New Jersey, Cretaceous Greensands.

ORIGINAL TYPE DESCRIPTION.—“The other specimens consist of an entire dermal scale and the half of a second, from the Green Sand formation of Mount Holly, New Jersey. These belong to some Crocodilian reptile of large size. They are deeply sculptured, but possess no carina, as in the existing Crocodiles. Possibly they may belong to the Saurian, characterized from some vertebræ under the name of *Cimoliasaurus magnus* . . . *Leidy*, but at present I prefer referring them to a new genus and species under the name of *Thoracosaurus grandis*.

Long diameter of the entire scale,.....	3½ inches.
Short “	3 “
Greatest thickness.....	7 lines.”

Provisionally referred to *T. neocesariensis* (De Kay), following Hay.

Thoracosaurus (Crocodilus) dekayi (Leidy)

ORIGINAL TYPE REFERENCE.—LEIDY, J., 1852, ‘Description of a new Species of Crocodile from the Miocene of Virginia,’ Journ. Acad. Nat. Sci. Phila., II, Ser. 2, p. 135, (*Crocodilus dekayi*).

SUBSEQUENT REFERENCES.—DE KAY, J. E., 1833, ‘Observations on a Fossil Jaw of a Species of Gavial, from West Jersey,’ Ann. Lyc. Nat. Hist., N. Y., III, pp. 156–165, Pl. III, figs. 7–10, (“Gavial”). TOULA, F., AND KAIL, J. A., 1885, ‘Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,’ Denkschr. k. Akad. Wissensch. Wien, p. 354, (*Crocodilus DeKayi*). HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 515, (*Thoracosaurus neocesariensis*).

ORIGINAL TYPE FIGURES.—DE KAY, J. E., 1833, ‘Observations on a Fossil Jaw of a Species of Gavial, from West Jersey,’ Ann. Lyc. Nat. Hist. N. Y., III, Pl. III, figs. 7–10.

TYPE.—Parts of a jaw. The type of *Thoracosaurus neocesariensis* (De Kay).

TYPE LOCALITY AND LEVEL.—Southern New Jersey, Cretaceous marls.

ORIGINAL TYPE DESCRIPTION.—“Dr. Dekay . . . has described several fragments of an inferior maxilla of a species of Gavial found in the Green-sand formation of the

southern part of New Jersey. It is undoubtedly different from the *Crocodylus macrohynchus*, *Harlan*, and also the gavial-like *Crocodylus clavirostris*, *Morton*. It may probably belong to one of two species of *Crocodylus*, since characterised by Mr. Owen, . . . of London, from several vertebræ found in the same formation, which of course can only be inferred from relations of size. In the present state of uncertainty whether these fragments of fossil jaw belong to an animal different from any before characterised, it will not be improper to apply to it the name *Crocodylus Dekayi*, in honor of Dr. Dekay, who has so well described the specimens, because a synonyme, should the species on further discovery prove not to be new, would produce much less inconvenience, than a want of a name at present for convenient reference."

Synonym of *Thoracosaurus neocesariensis* (De Kay), which was founded on the same type specimen.

PLIOGONODON Leidy

ORIGINAL TYPE REFERENCE.—LEIDY, J., 1856, 'Notices of Remains of Extinct Vertebrated Animals discovered by Professor E. Emmons,' Proc. Acad. Nat. Sci. Phila., VIII, p. 255; also 1857, Amer. Journ. Sci. and Arts, Ser. 2, XXIII, pp. 271, 272.

SUBSEQUENT REFERENCE.—HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 517.

TYPE.—*Pliogonodon priscus* Leidy.

ORIGINAL TYPE DESCRIPTION.—No distinction was made by Leidy between the characters of the genus and those of the type species. See *Pliogonodon priscus*.

The position of this genus is uncertain.

Pliogonodon priscus Leidy

ORIGINAL TYPE REFERENCE.—LEIDY, J., 1856, 'Notices of Remains of Extinct Vertebrated Animals discovered by Professor E. Emmons,' Proc. Acad. Nat. Sci. Phila., VIII, pp. 255, 256; also 1857, Amer. Journ. Sci. and Arts, Ser. 2, XXIII, pp. 271, 272.

SUBSEQUENT REFERENCES.—EMMONS, E., 1858, 'Report of the North Carolina Geological Survey. Agriculture of the Eastern Counties; together with Descriptions of the Fossils of the Marl Beds,' North Carolina Geol. Surv., pp. 223, 224, figs. 43, 44, (*Pliogonodon nobilis*). LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, pp. 103, 119. COPE, E. D., 1875, 'Report of the Geological Survey of North Carolina Volume I, by W. C. Kerr,' Appendix B, p. 33, North Carolina Geol. Surv., I. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 517.

ORIGINAL TYPE FIGURES.—EMMONS, E., 1858, 'Report of the North Carolina Geological

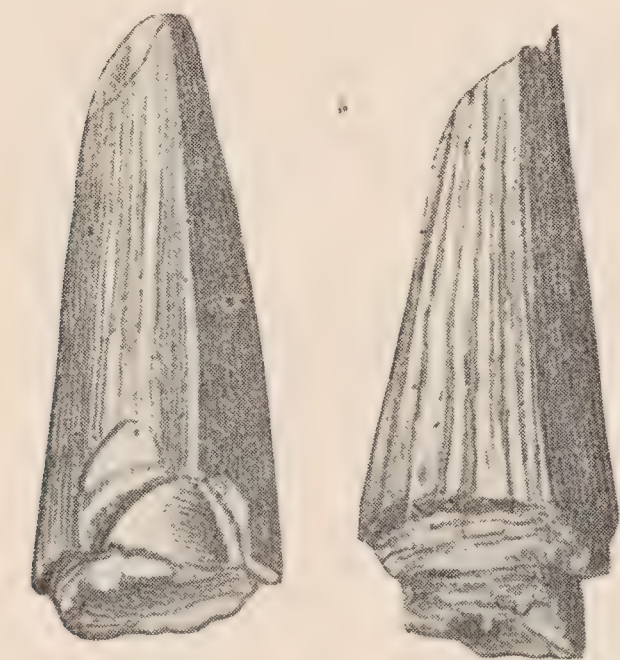


Fig. 19. *Pliogonodon priscus* Leidy. Type specimen, teeth.

Natural size. Original type figures. (After Emmons.)

Survey. Agriculture of the Eastern Counties; together with Descriptions of the Fossils of the Marl Beds,' North Carolina Geol. Surv., figs. 43, 44.

TYPE.—Two mutilated teeth.

TYPE LOCALITY AND LEVEL.—Cape Fear, North Carolina. Miocene (?) Beds.

ORIGINAL TYPE DESCRIPTION.—“Teeth elongated conical, nearly straight or only slightly curved inwardly, in section circular, with a pair of opposed carinæ on the inner side; surfaces divided into numerous narrow planes, with a few vertical interrupted plicæ, which are more numerous on the inner side. Enamel finely wrinkled; and the dentine concentric. Base of crown hollowed. Probable length of crown when perfect 2 inches, breadth of base $\frac{3}{4}$ of an inch.

The teeth differ from those of *Mosasaurus* in their narrower proportion, straightness, circular section, and the plicæ of the enamel; from those of *Polyptychodon* in the possession of divisional planes and opposed carinæ; and from those of *Pleiosaurus* in the former character and the circular section.”

No adequate determination can be made at the present time.

HOLOPS Cope

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1869, [Remarks on *Holops brevispinus*, *Ornithotarsus immanis*, and *Macrosaurus proriger*], Proc. Acad. Nat. Sci. Phila., XXI, p. 123.

SUBSEQUENT REFERENCES.—COPE, E. D., 1869, ‘Synopsis of the Extinct Batrachia and Reptilia of North America,’ Trans. Amer. Phil. Soc., N.S., XIV, Part 1, Art. 1, pp. 26, 27, 28, 231. HUXLEY, T. H., 1875, ‘On Stagonolepis robertsoni, and on the Evolution of the Crocodilia,’ Quart. Journ. Geol. Soc. London, XXXI, pp. 423–438. MARSH, O. C., 1877, ‘Introduction and Succession of Vertebrate Life in America,’ Amer. Journ. Sci. and Arts, Ser. 3, XIV, Art. 42, p. 346. LYDEKKER, R., 1886, ‘Siwalik Crocodilia, Lacertilia, and Ophidia,’ Mem. Geol. Surv. India, Palæontologia Indica, Ser. 10, III, Part 7, pp. 3 (211), 12 (220), 17 (225), 27 (235). NICHOLSON, H. A., AND LYDEKKER, R., 1889, ‘A Manual of Palæontology for the Use of Students with a General Introduction on the Principles of Palæontology,’ p. 1193. ZITTEL, K. VON, 1890, ‘Handbuch der Palæontologie,’ Abth. 1, Palæozoologie, III, Vertebrata, p. 673. COPE, E. D., 1900, ‘The Crocodilians, Lizards, and Snakes of North America,’ Rept. U. S. Nat. Mus. for 1900, p. 162. HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 515. WILLISTON, S. W., 1906, ‘American Amphicoelian Crocodiles,’ Journ. Geol., XIV, pp. 2, 17; 1914, ‘Water Reptiles of the Past and Present,’ p. 207. SELLARDS, E. H., 1915, ‘A New Gavial from the Late Tertiary of Florida,’ Amer. Journ. Sci., Ser. 4, XL, p. 137.

TYPE.—*Thoracosaurus brevispinus* Cope.

ORIGINAL TYPE DESCRIPTION.—“Prof. Cope exhibited some specimens of extinct reptiles of interest. One of these was the cranium, minus a portion of the muzzle of a gavial, from the New Jersey Green Sand, previously described under the name of *Thoracosaurus brevispinus*, but which this specimen demonstrated to belong to another genus, since it did not present the lachrymal foramina of the former. He applied the name *Holops* to it, and stated that he had evidence that *Crocodylus tenebrosus* Leidy, and probably *C. obscurus* L., also belonged to it.” (Minutes of meeting of the Academy of Natural Sciences of Philadelphia for June 1, 1869).

The genus may provisionally be considered valid.

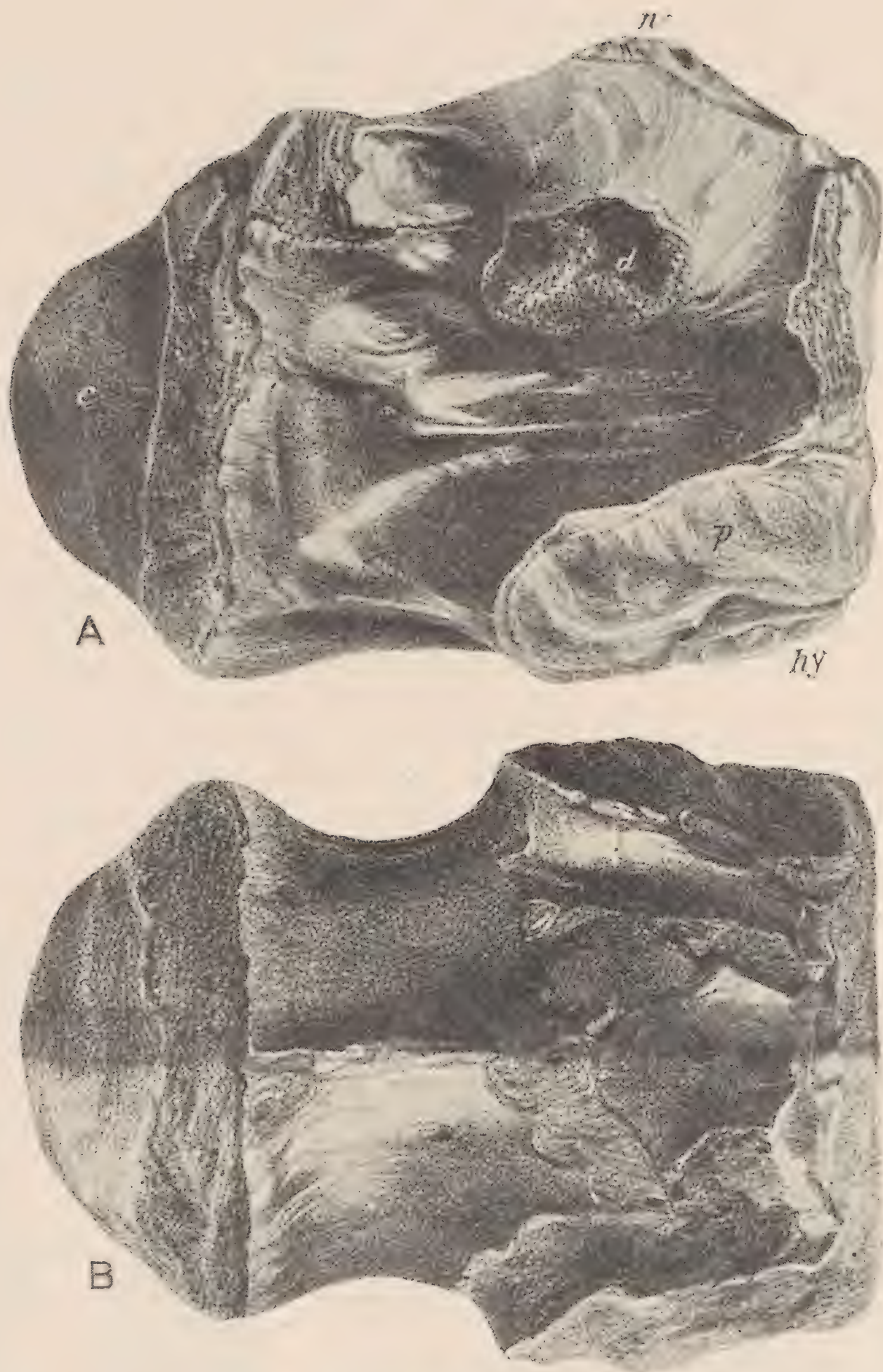


Fig. 20. *Holops basitruncatus* (Owen). Type specimen, fourth or fifth cervical vertebra.

Scale not indicated by Owen, and no measurements are given. Presumably the figures are natural size. A, lateral view, right side; B, inferior view; *c*, posterior ball of centrum; *d*, base of diapophysis; *hy*, base of hypapophysis; *n*, base of neural arch; *p*, base of parapophysis. Original type figures. (After Owen.)

Holops basitruncatus (Owen)

ORIGINAL TYPE REFERENCE.—OWEN, R., 1849, 'Notes on Remains of Fossil Reptiles discovered by Prof. Henry Rogers of Pennsylvania, U. S., in Greensand Formations of New Jersey,' Quart. Journ. Geol. Soc. London, V, p. 381, Pl. x, figs. 3, 4, (*Crocodylus basitruncatus*).

SUBSEQUENT REFERENCES.—GIBBES, R. W., 1852, 'A Memoir on *Mosasaurus* and the three Allied New Genera, *Holcodus*, *Conosaurus*, and *Amphorosteus*,' Smith. Contrib. Knowl., II, Art. 5, p. 13, (*Crocodylus basitruncatus*). LEIDY, J., 1852, 'Description of a new Species of Crocodile from the Miocene of Virginia,' Journ. Acad. Nat. Sci. Phila., VI, p. 135, (*Crocodylus basitruncatus*). OWEN, R., 1860, 'On the Orders of Fossil and Recent Reptilia, and their Distribution in Time,' Rept. Brit. Assoc. Adv. Sci. for 1859, p. 165, (*Crocodylus basitruncatus*). LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, pp. 14, 115, Pl. III, figs. 12–15, (*Crocodylus basitruncatus*, *C. tenebrosus*). COPE, E. D., 1869, 'Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,' in 'Geology of New Jersey,' by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736, (*T. tenebrosus*); 1869, [Remarks on *Holops brevispinus*, *Ornithotarsus immanis* and *Macrosaurus proriger*], Proc. Acad. Nat. Sci. Phila., XXI, p. 123, (*Crocodylus tenebrosus*); 1869, 1870, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N.S., XIV, pp. 67, 77–79, 231, fig. 19 (according to Hay), Pl. IV, figs. 8, 9 (according to Hay), 1869 (pp. 67, 77–79), 1870 (p. 231), (*Crocodylus basitruncatus* and *Holops tenebrosus*); 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge II, pp. 253. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515.

ORIGINAL TYPE FIGURES.—OWEN, R., 1849, 'Notes on Remains of Fossil Reptiles discovered by Prof. Henry Rogers of Pennsylvania, U. S., in Greensand Formations of New Jersey,' Quart. Journ. Geol. Soc. London, V, Pl. x, figs. 3, 4.

TYPE.—Cervical vertebra, fourth or fifth, selected by Owen from a large series.

TYPE LOCALITY AND LEVEL.—New Jersey, Upper Cretaceous Greensands.

ORIGINAL TYPE DESCRIPTION.—"The most marked difference between the vertebræ figs. 1 & 3 is presented by the latter process [hypapophysis]: in fig. 1 it is double, or divided by a median longitudinal cleft; in fig. 2 it is single, broad, flattened and smooth below. These characters are well and accurately shown in the figs. 2 & 4 of the inferior surface of the vertebræ selected. A corresponding modification of the hypapophysis was presented by other cervical and anterior dorsal vertebræ of each series respectively. But the specific distinction of the two is manifested by other characters. The cervical vertebra, figs. 3 & 4, is longer in proportion to its breadth than figs. 1 & 2: the parapophysis, *p* in fig. 1, comes off from the middle of the side of the centrum: in fig. 3 its origin is more advanced, and extends to the border of the anterior articular cup. And these characters were not those distinguishing different positions of the vertebræ in the same cervical series, any more than those of the hypapophyses, but were characteristic of the other cervical vertebræ of each series respectively.

Two species therefore, of Crocodile or Alligator, were thus established, equalling in size the existing *Alligator lucius* of the Southern States, or the *Crocodilus acutus* of Jamaica.

For the species characterized by vertebræ of the type of that depicted in figs. 1 & 2, I propose the name of *Crocodilus basifissus*; for the species with the inferior process single, short and flattened, that of *Crocodilus basitruncatus*."

The species may provisionally be considered valid.

Holops obscurus (Leidy)

ORIGINAL TYPE REFERENCE.—LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, pp. 15, 16, 115, Pl. II, figs. 4, 5, (*Crocodilus obscurus*).

SUBSEQUENT REFERENCES.—COPE, E. D., 1867, 'The Fossil Reptiles of New Jersey,' Amer. Nat., I, p. 26, (*Thoracosaurus obscurus*); 1869, 'Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,' in 'Geology of New Jersey,' by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736, (*Thoracosaurus obscurus*); 1869, [Remarks on *Holops brevispinus*, *Ornithotarsus immanis* and *Macrosaurus proriger*], Proc. Acad. Nat. Sci. Phila., XXI, p. 123, (*Crocodilus obscurus*); 1869, 1870, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N.S., XIV, Part 1, pp. 68, 75-78, 231, Pl. IV, figs. 1-3; 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, p. 253. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354,

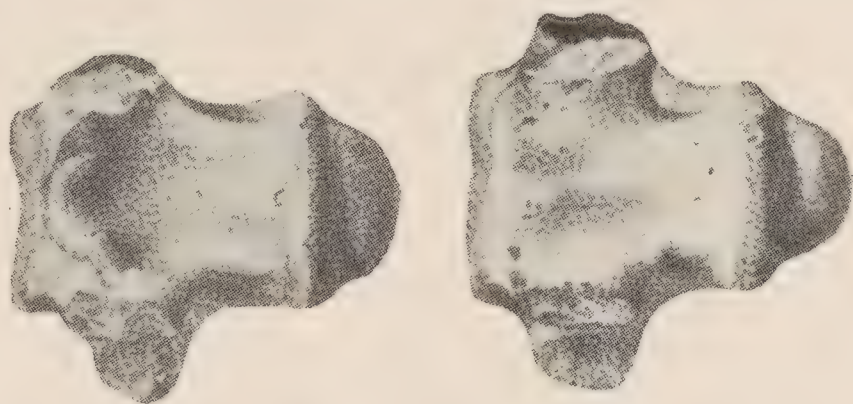


Fig. 21. *Holops obscurus* (Leidy). Co-type specimen, cervical vertebræ, probably fourth and fifth (Geol. Mus. Rutgers College Coll.).

One-half natural size, inferior views. Original type figures. (After Leidy.)

(*Crocodilus obscurus*). LYDEKKER, R., 1886, 'Siwalik Crocodilia, Lacertilia, and Ophidia,' Mem. Geol. Surv. India, Palæontologia Indica, Ser. 10, III, Part 7, p. 211. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 516.

ORIGINAL TYPE FIGURES.—LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, Pl. II, figs. 4, 5 (Leidy figures on Pl. I, figs. 7-9, some teeth with the caption "Gavial from New Jersey." Hay subsequently referred to these as *H. obscurus*).

COTYPES.—Four vertebræ, the shaft of a femur, and four dermal bones, from Barnesboro, New Jersey, in Geol. Mus. Rutgers College; two posterior dorsal or lumbar vertebræ, from Arneytown, New Jersey, in Acad. Nat. Sci. Phila. Coll.

TYPE LOCALITIES AND LEVEL.—The first specimen from Barnesboro, Gloucester County, the second from Arneytown, Burlington County, New Jersey. Upper Cretaceous Greensands.

ORIGINAL TYPE DESCRIPTIONS.—“Recently Prof. Cook has sent to me for examination a small collection of Crocodile bones belonging to the collection of Rutger’s College. The specimens were obtained from near Barnesboro’, Gloucester County, N. J., and consist of four vertebræ, the shaft of a femur, and four broken dermal bones, apparently all from the same individual.

The vertebræ have had their arches fully coossified with the bodies, so that they may be considered as having belonged to an animal of mature age. They belonged to a smaller individual than the specimens above described, and perhaps to a different species, for several present some peculiarities of form.

Two of the vertebræ, Figs. 4, 5, Plate II, belonged in the cervical series between the fourth and last, and are probably the fourth and fifth. The bodies measure an inch and three-quarters in length, independent of their posterior convexity, and correspond in general form with those of the Alligator. The hypapophysis of the fourth, Fig. 4, is a thick semicircular ridge extending between and below the level of the parapophyses. In the fifth, Fig. 5, it is a longer, straighter, and less well developed ridge, slightly notched in the middle.

The other two vertebræ are the first and fifth dorsal, and have their body about as long as the cervicals. The first dorsal has lost its hypapophysis, spinous process, and portions of the others, but so far as it is preserved it corresponds in form with that of the Alligator. The fifth dorsal has its body more compressed laterally than in the specimen above described from Timber Creek, and the hypapophysis is absolutely very much more robust than in the latter, though the vertebra is smaller. In the Barnesboro’ specimen the anterior articular concavity of the body is quadrilateral, whereas it is broadly cordiform in the Timber Creek specimen. In the former the hypapophysis is excavated in front; in the latter it is plane. These differences in two characteristic vertebræ are, perhaps, sufficient to indicate that they belong to two species.

Comparative measurements of the two vertebræ are as follows:—

	BARNES- BORO’ SP.	TIMBER CREEK SP.
	Lines.	Lines.
Length of body inferiorly.....	20	22
Length of body laterally.....	20	22
Height of body anteriorly.....	17	18
Width of body anteriorly.....	16	22
Thickness of body at middle.....	12	17
Thickness of hypapophysis.....	9	6
Breadth of vertebral arch laterally . . .	17	20
Width of vertebral canal.....	6	7
Height of vertebral canal.....	7	8

The specimen of the shaft of a femur is three inches and a third in circumference, and resembles the corresponding portion of the same bone in the Alligator.

The dermal bones are square, differ in size, and are coarsely foveated. Two of them form a median elevation without being carinated; the others are flat. One of the more perfect measures two inches by twenty lines; another measures two inches eight lines by two inches.

The museum of the Academy contains two mutilated bodies of posterior dorsal or of lumbar vertebræ, of mature age, from Arneytown, Burlington County, N. J., presented by T. A. Conrad. The specimens, excepting in being devoid of the hypapophysis, agree with the bodies of the dorsals above described, and are like those in the living Alligator."

The species may provisionally be considered valid.

Holops (*Crocodylus*) *tenebrosus* (Leidy)

ORIGINAL TYPE REFERENCE.—LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, pp. 14, 15, 115, Pl. III, figs. 12-15, (*Crocodylus tenebrosus*).

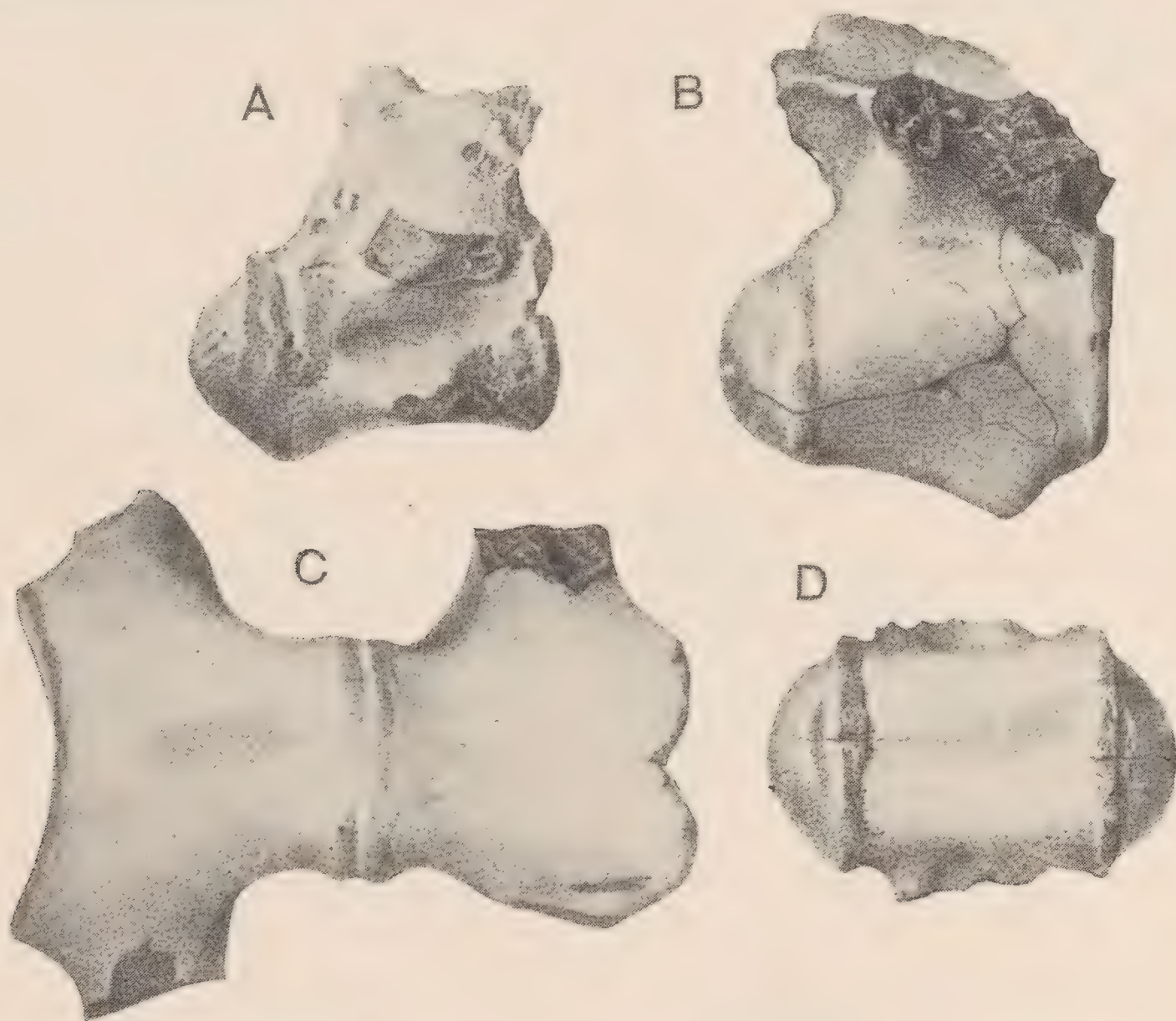


Fig. 22. *Holops (Crocodylus) tenebrosus* (Leidy). Type specimen, vertebræ (Acad. Nat. Sci. Phila. Coll.).

One-half natural size. A, sixth cervical vertebra, lateral view, right side; B, fifth dorsal vertebra, lateral view, right side; C, sacral vertebræ, inferior view; D, first caudal vertebra, inferior view. Original type figures. (After Leidy.)

SUBSEQUENT REFERENCES.—COPE, E. D., 1869, 'Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,' in 'Geology of New Jersey,' by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736, (*Thoracosaurus tenebrosus*); 1869, 'Synopsis of the Extinct Batrachia and Reptilia of North

America,' Trans. Amer. Phil. Soc., N.S., XIV, Part 1, p. 78. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515, (*Holops basitruncatus*).

ORIGINAL TYPE FIGURES.—LEIDY, J., 1865, 'Cretaceous Reptiles of the United States,' Smith. Contrib. Knowl., XIV, Pl. III, figs. 12-15.

TYPE.—Two cervical, a dorsal, a sacral and two caudal vertebræ, and portions of both humeri. Acad. Nat. Sci. Phila. Coll.

TYPE LOCALITY AND LEVEL.—Timber Creek, Gloucester County, New Jersey. Cretaceous Greensand beds.

ORIGINAL TYPE DESCRIPTION.—"Of other remains of Crocodiles, with vertebræ constructed on the same plan as the living representatives of the family, I have seen a number of specimens from the Green-sand of New Jersey apparently indicating several species different from the preceding [*Bottosaurus harlani*]. Among these is a collection of bones belonging to the same individual, from Timber Creek, Gloucester County, N. J., presented to the Academy by W. P. Foulke. They consist of two cervical, a dorsal, the sacral, and two caudal vertebræ, and portions of both humeri. The vertebræ indicate an adult animal, as the arches are completely united with their respective bodies, and those of the sacrum are firmly coossified. Their comparatively small size renders it improbable that they should belong to either of the species previously indicated [*Thoracosaurus neocesariensis* and *Bottosaurus harlani*].

The bones are black, heavy, and firm, but unfortunately the vertebræ have had most of their processes broken off since their discovery.

The least mutilated of the cervical vertebræ, apparently the sixth, represented in Fig. 12, Plate III, is rather less than two inches in length, independent of the articular convexity of its body. Inferiorly, the latter is divided by a median carina expanding in front into a broad flat space without a distinct hypapophysis, otherwise the specimen presents nothing remarkable by which to characterize it. The other vertebræ of the neck, apparently a fourth or fifth, has the inferior carina of the body almost obsolete—commencing in a small tubercle behind, and fading away as it approaches a concavity extending between the parapophyses or inferior transverse processes. The latter are more robust than in the former specimen, and appear to have been conjoined by a ridge-like hypapophysis, though this is too much broken to judge of its true character.

The dorsal vertebra, Fig. 13, Plate III, the fifth of the series, has about the same length as those of the neck, and is nearly as broad anteriorly as it is long. Its hypapophysis is a robust mammillary tubercle, but it is otherwise like the corresponding bone of the common Alligator.

The conjoined bodies of the sacral vertebræ, represented in Fig. 14, Plate III, relate in size with the preceding, and differ in no important point with the homologous parts of the Alligator.

Of the caudal vertebræ, one is the first of the series, distinguished by the double articular convexity of the body, as seen in Fig. 15, Plate III. Unlike that of the Alligator, it is broad and flattened beneath, resembling in this respect more the condition of the bodies of the sacral vertebræ. The second specimen, from near the middle of the tail, is much mutilated. It measures rather more than two inches in length, and appears to have had the same form as in the Alligator.

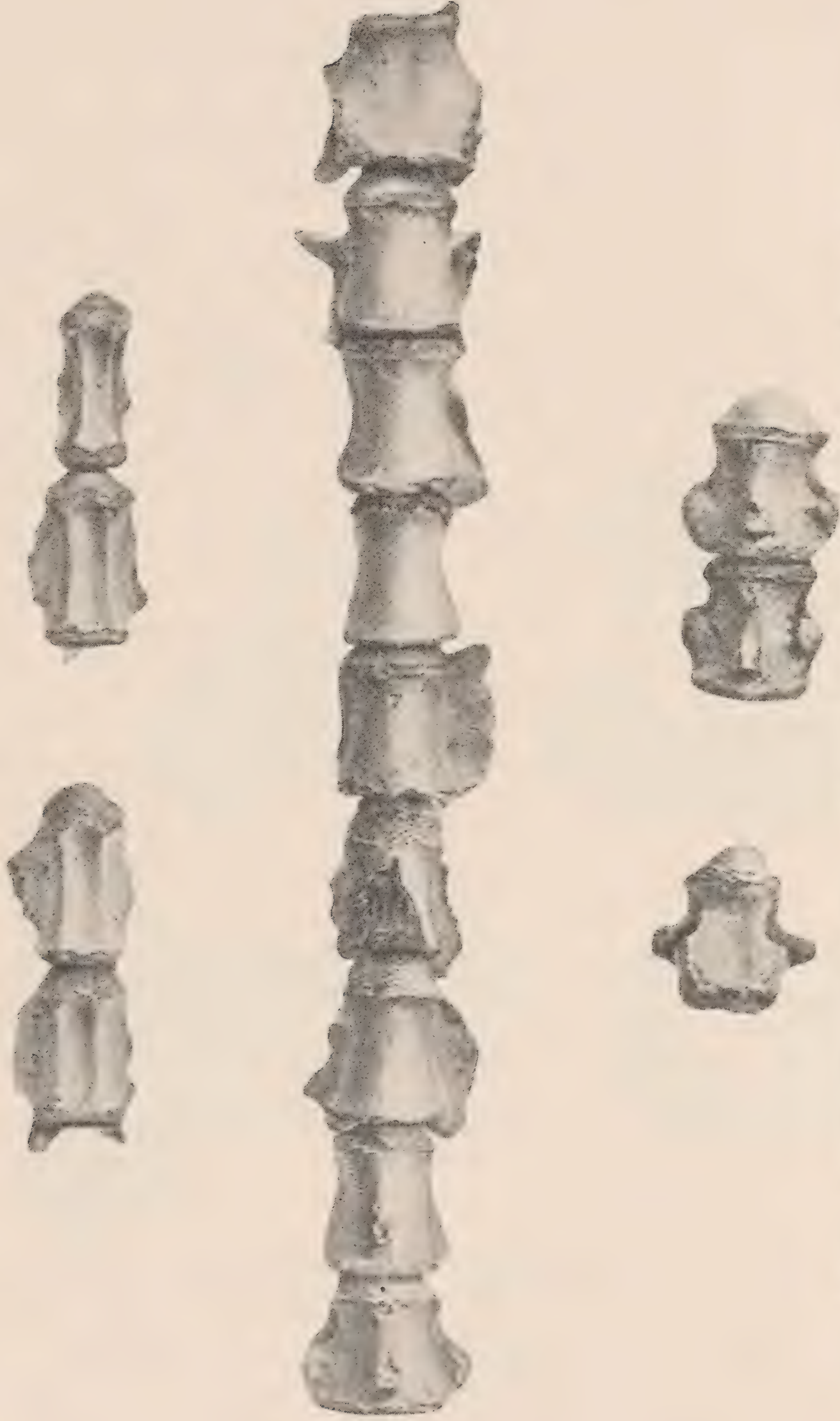


Fig. 23. *Holops brevispinus* (Cope). Type specimen, vertebrae from various parts of the column.
One-half natural size. Inferior views. Original type figures. (After Cope.)

Of the fragments of humeri, one consists of a portion of the shaft of that of the right side, and measures three inches in circumference; the other is the proximal extremity of the left humerus, and does not differ from the corresponding part in the Alligator. Its head measures rather more than two inches in its greater diameter, and a little more than one inch in its lesser diameter."

Hay lists this species under *Holops basitruncatus*; this determination may be followed provisionally.

Holops brevispinus (Cope)

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1867, [Note on *Thoracosaurus brevispinus*], Proc. Acad. Nat. Sci. Phila., XIX, p. 39, (*Thoracosaurus brevispinus*).

SUBSEQUENT REFERENCES.—COPE, E. D., 1869, 'Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,' in 'Geology of New Jersey,' by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736, (*Thoracosaurus brevispinus*); 1869, [Remarks on *Holops brevispinus*, *Ornithotarsus immanis*, and *Macrosaurus proriger*], Proc. Acad. Nat. Sci. Phila., XXI, p. 123; 1869, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N.S., XIV, Part 1, pp. 68-73, Pl. I, fig. 13, Pl. IV, figs. 4-6, (*Holops brevispinus*); 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, p. 252. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 516, (*Holops brevispinis*).

ORIGINAL TYPE FIGURES.—COPE, E. D., 1875, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N.S., XIV, part 1, Pl. I, fig. 13, Pl. IV, figs. 4-6.

TYPES.—(Cope, 1867) "several vertebræ of a Gavial from the cretaceous marl of Burlington Co., N. J., and proposed for the new species the name of *Thoracosaurus brevispinus*"; (Cope, Trans. Amer. Philos. Soc., 1869) "The specimens on which this species are established are, a cervical vertebra in the Museum of the Academy of Natural Sciences, procured by Timothy A. Conrad at St. George's, Delaware, and one cervical, six dorsal, four lumbar, one sacral and four caudal vertebræ from the Greensand of Burlington County, N. J., which have been liberally placed at my disposal by the Burlington County Lyceum of Natural and Civil History. The last series is from the same individual apparently, and is more complete than that of any other cretaceous Crocodile hitherto brought to light. Also on a seventh dorsal, two lumbar and a humerus from the marl excavations of Samuel Engle, near Medford, Burlington County, New Jersey." The vertebræ submitted by the Burlington County Lyceum evidently constitute the material referred to in Cope's original announcement in 1867. Cope's first description, however, refers to a cranium, which is discussed in the article in the transactions of the American Philosophical Society as follows: "A mass of indurated marl, with vivianite and oxide of iron from Monmouth County, N. J., submitted to me by Prof. G. H. Cook, contains the posterior part of the cranium of this species, with cervical, dorsal, lumbar and caudal vertebræ, dermal plates and coracoids. The individual was immature, as shown by the non-anchylosis of the centrum of the atlas, the neural arches, etc." In the first adequate description of this

material and of this species (the 1869 article in the Transaction of the American Philosophical Society), all the material was described.

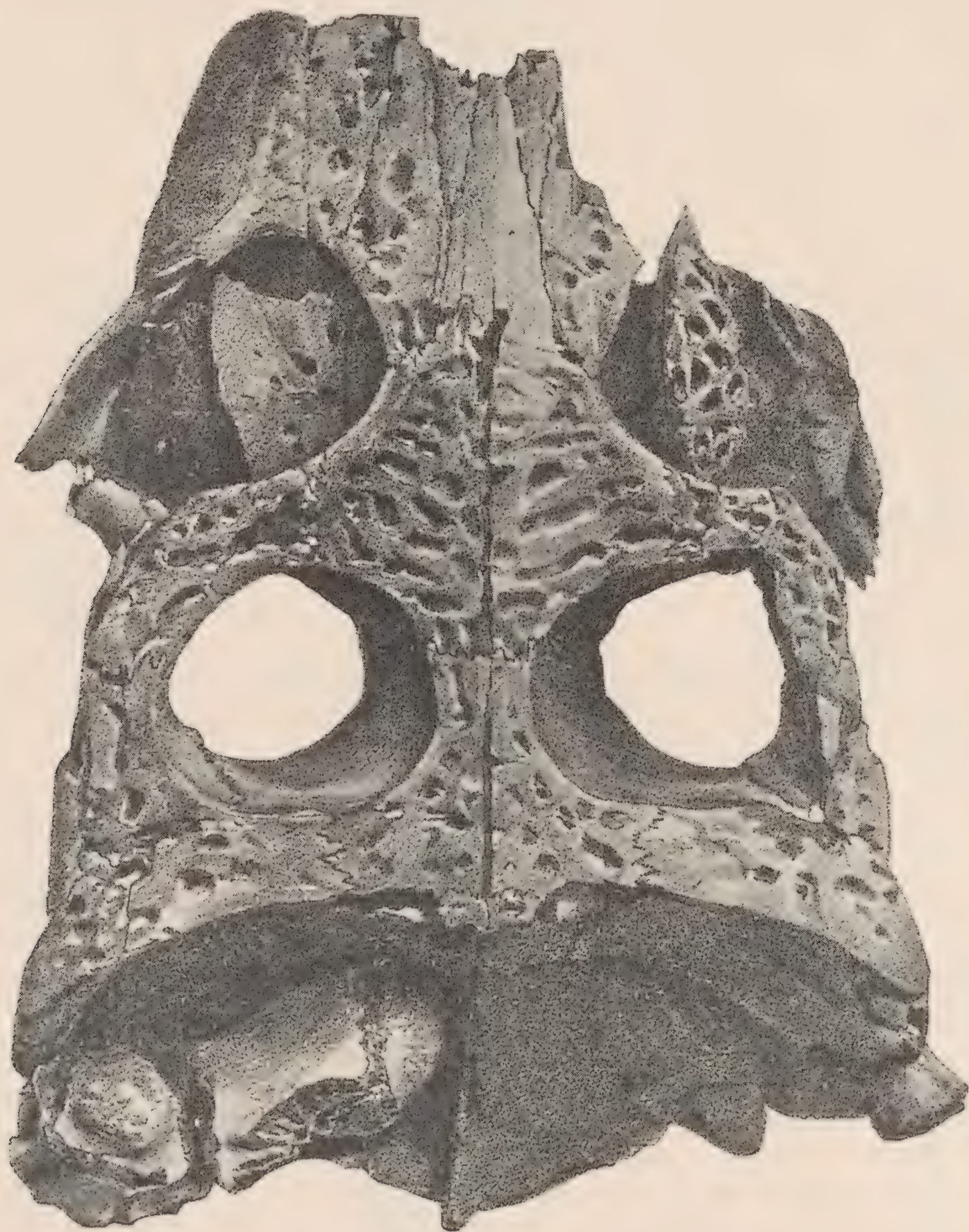


Fig. 24. *Holops brevispinus* (Cope). Hypotype specimen, posterior part of skull (Geol. Mus. Rutgers College Coll.).

Three-fourths natural size. Superior view. Original type figure. (After Cope.)

The vertebræ of the Burlington County Lyceum may be considered as the type, the vertebra from Delaware, and the vertebræ and humerus from near Medford as paratypes, and the cranium and associated material from Monmouth County as hypotype.

TYPE LOCALITIES AND LEVELS.—The type is from Burlington County, New Jersey; the paratypes are from St. George's, Delaware, and Burlington County,

New Jersey; and the hypotype is from Monmouth County, New Jersey; all from upper Cretaceous Greensands.

ORIGINAL TYPE DESCRIPTIONS.—Cope’s 1867 account consists merely of notes in the minutes of the meeting of the Philadelphia Academy of April 9, 1867: “Prof. Cope exhibited several vertebræ of a Gavial from the cretaceous marl of Burlington Co., N. J., and proposed for the new species the name of *Thoracosaurus brevispinus*.” In the proceedings of the Academy the following notes on the meeting of June 1, 1869, are recorded: “Prof. Cope exhibited some specimens of extinct reptiles of interest. One of these was the cranium, minus a portion of the muzzle of a gavial, from the New Jersey Green Sand, previously described under the name of *Thoracosaurus brevispinus*, but which this specimen demonstrated to belong to another genus, since it did not present the lachrymal foramina of the former. He applied the name *Holops* to it, and stated that he had evidence that *Crocodylus tenebrosus* Leidy, and probably *C. obscurus* L., also belonged to it.”

The first adequate description of the species by Cope is found in the 1869 article in the Transactions of the American Philosophical Society. It is quoted in full as follows:

“The last are from an adult, while the more perfectly preserved is not fully grown, since the neural arches of many of the dorsal vertebræ have separated at their sutures, yet its approach to maturity is indicated by the persistence of this arch of the third cervical, of some dorsals, lumbar and caudals. The species is the smallest of the genus, and will furnish reliable data for the estimation of the dimensions of other extinct crocodilia. The vertebræ are relatively more slender than those of the Alligators, and the general proportions are more probably those of the *T. neocaesariensis* and of the Gavials.. This will give a basis of estimation for the head and tail.

	Inches.
Length of cervical series,	7.75
“ dorsal “	15.
“ lumbar “	6.25
“ sacral “	2.33
Total body,	31.33
Caudal series (part estimated),	35.
Head (estimated),	13.
Total,	6 ft. 7½ inches.

Cervical vertebræ.—Characteristic of the two of these before us, is the deep concavity of the inferior aspect of the centrum with only a trace of a keel, and the steep elevation of the same surface to the rim of the articular cup. The latter does not form a well defined ridge, but rather a plane, connecting the anterior extremities of the parapophyses, which, in the sixth, supports two short acuminate hypapophyses. In both cervicals the parapophyses look outwards at right angles to the centrum, but as in existing species, possess shorter articular surfaces on the third, whose body is also rather more elongate behind them. In the sixth, which will be typical of the posterior four of the species of the series, from the crest of the posterior shoulder to the posterior outline of the parapophysis, is one-half the distance from the latter point to the margin of the anterior cup, and somewhat less than the articular face of the parapophysis

The posterior shoulder is elevated in both, and the articular globe is contracted and projecting.

The vertical diameter of the neural canal of the third is four-fifths the same as the anterior cup. The latter is small, its vertical diameter being only double the depth of the osseous elevation between the parapophyses. The neural spine is little elevated, compressed, its anterior margin subacute, and obliquely turned backwards to a posterior apex.

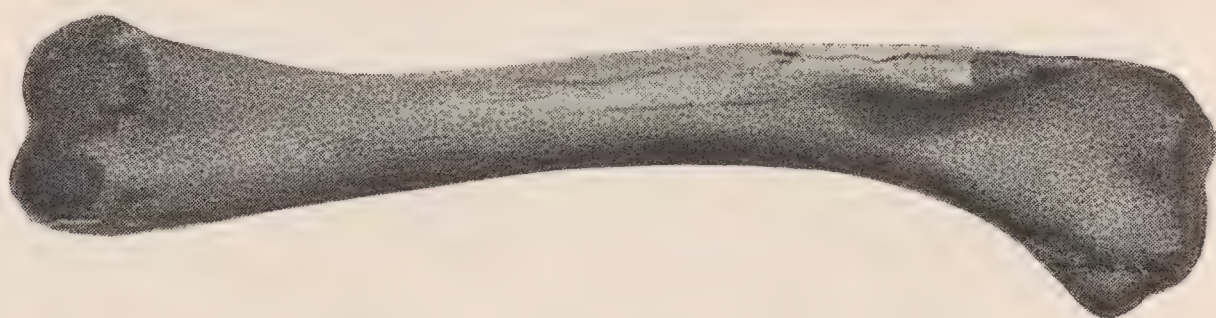


Fig. 25. *Holops brevispinus* (Cope). Paratype specimen, right humerus.

One-half natural size. Anterior view. Original type figure. (After Cope.)

Measurements.

	In.	Lin.
Third cervical, total length,	1	5.
Crest of shoulder to outer angle parapophysis,		6.5
Last point to plane of cup rim,		6.5
From middle ball of apex neural spine,	1	7.
Least width of base of centrum,		6.25
Sixth cervical (larger individual), length,	1	7.5
Vertical diameter between rims of cup,		10.5

The expanded bases of the neurapophyses leave only the cariniform epapophysis between them.

Dorsal vertebræ.—The first, third and fourth with the parapophysis on the centrum have lost only their neural arches. The parapophyses have convex articular surfaces, which have a very posterior direction and are followed by a deep depression in the side of the centrum; in the first they are a little behind the middle of the side of the body. The hypapophyses of all are distinguished by their lack of compression and their obtuseness. They are directed vertically downwards, the anterior face posteriorly. That of the first is bifid as broad as long, the others simple, longer than broad on the third. They are preceded by a depression behind the rim of the cup, and succeeded by a second, simple, small hypapophysis near the shoulder, which is finely many-grooved; it exists as a trace on the third, which of all the dorsals, may alone be said to present a very obtuse carina below. The surface in the first three is striate next the rim of the cup; on the shoulder on the first two. The sixth dorsal is more compressed and smoother; its cup is more produced upwards and outwards, while that of the first is more nearly round and the others are intermediate.

The articular cups of dorsals near the seventh and eighth are nearly round, slightly deeper than broad. The horizontal width of the diapophyses is considerable, and the transverse extent of the articular (inferior) surface of the posterior zygapophysis is equal one-half the length of the centrum between shoulder and cup.

The seventh dorsal of the adult is perhaps twice as large as the above, without being half as large as the same in the *H. obscurus*. Though the centrum is as much compressed as that of the sixth, the cup is still broader than deep vertically. The centrum has a lateral longitudinal obtuse ridge. The hypapophysis is remarkably large for the position in the vertebral column. It is trigonal in profile with truncate planes before and behind, the anterior concave. The costal articular face is half way to the extremity of the diapophysis on its anterior margin. It is transverse, not vertical as in the sixth in *H. tenebrosus*.

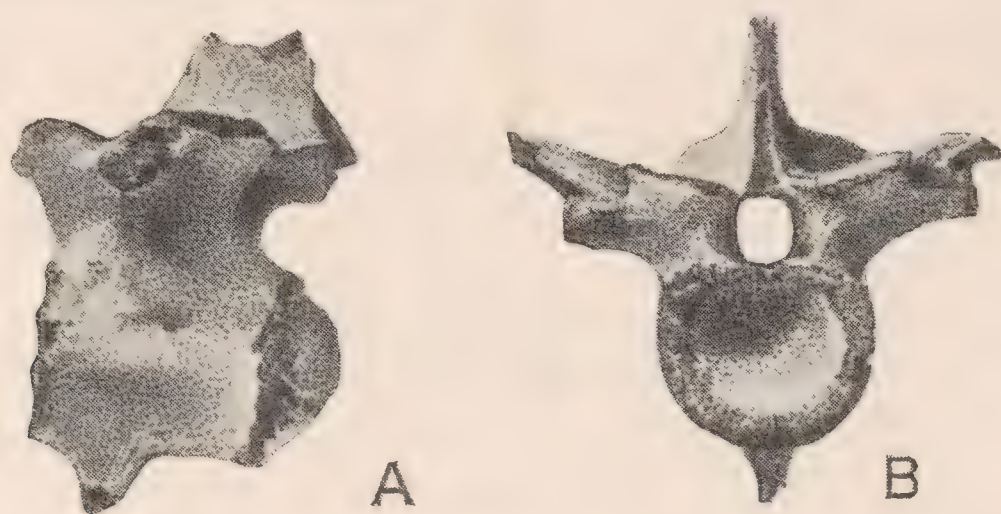


Fig. 26. *Holops brevispinus* (Cope). Paratype specimen, anterior dorsal vertebra.

One-half natural size. A, lateral view, left side; B, anterior view. Original type figures. (After Cope.)

Sacral.—The first exhibits a longitudinal concavity on the posterior half of the centrum below.

Caudals.—The body of an anterior caudal is not compressed, those of three others, but slightly so; the cup of the first is round; those of the others deeper than broad. Three have stout diapophyses; of these the two posterior have a concave inferior face separated by a strong angle from the sides, while there is an additional lateral angulation on the anterior part of the side of the more anterior. In the two anterior, the neural spine is twice constricted from base probably to near apex, leaving an anterior laminiform portion, and a median much stouter. In the caudals the suture of the neural arch is much obliterated.

Measurements of Vertebræ.

Of Adult.

	<i>In.</i>	<i>Lin.</i>
Seventh dorsal; total length,	1	8.
depth articular cup,		10.5
width,		12.
longitudinal width neural arch (greatest),	1	8.
“ “ diapophysis,		11.

Of Young.

	<i>In.</i>	<i>Lin.</i>
Sixth dorsal; total length,	1	5.
length to shoulder,	1	1.5
depth neural canal to end hypapophysis,	1	1.5
“ articular cup,		9.25
width “ “		11.

Measurements of Vertebræ.

. Of Young.

	<i>In.</i>	<i>Lin.</i>
Eighth ? dorsal; total length,	1	5.
length to shoulder,	1	1.
longitudinal line between zygapophyses,	1	5.5
horizontal base of neural spine,		11.
depth of neural canal,		4.5
" " articular cup,		9.5
width of " "		9.5
neural suture to nearest diapophysis,		3.
Third ? lumbar; total length,	1	5.
length to shoulder,	1	1.
longitud. line between zygapophyses,	1	6.
horizontal base of neural spine,	1	
depth neural canal,		4.75
" articular cup,		9.
width " "		11.
First sacral; length,	1	2.75
anterior width centrum,	1	.75
posterior " "		10.
depth neural canal,		4.75
" articulation of diapophysis		11.
length " " "		9.
width neural arch between diapophyses,	1	2.5
Anterior caudal; length,	1	5.
" to shoulder,	1	1.5
depth neural canal,		4.5
" articular cup,		8.
width " "		8.75
width inferior plane,		4.
Distal caudal; length,	1	5.5
" to shoulder,	1	3.25
depth cup, ¹		6.
width "		5.
length base diapophysis,		3.75

None of the vertebræ exhibit a constriction of the neural canal by a ridge on each of its sides, as is seen in the *H. tenebrosus*.

This specimen is named from the short longitudinal and vertical extent of its hypapophyses.

A right *humerus* accompanying three vertebræ of the adult, has the same color and mineralization, and was found with them; it probably belongs to the same animal. Compared with a humerus of *H. obscurus* of medium size, it is three-fifths the length and has more strongly marked articular faces. The head is more transverse, less rounded, and more strongly divided into the scapular and coracoid faces. The width of the head is one-fourth the length, and reaches the summit of the deltoid

¹Measurements of the articular cup are always made from middle to middle of the rim."

crest. This crest is lower down in *H. obscurus*, the above width only reaching its proximal base. The anterior face above the crest is concave in *H. brevispinis*, nearly flat in *H. obscurus*. There is a moderate internal tuberosity distally, and the condyles are moderately prominent. Coronoid fossa well marked.

	<i>In.</i>	<i>Lin.</i>
Length,	6	8.
" to middle of deltoid crest,	1	8.5
Width of head,	1	7.
" shank at middle,		8.5
" condyles,		17.5

A mass of indurated marl, with vivianite and oxide of iron from Monmouth County, N. J., submitted to me by Prof. G. H. Cook, contains the posterior part of the cranium of this species, with cervical, dorsal, lumbar and caudal vertebræ, dermal plates and coracoids. The individual was immature, as shown by the non-anchylösis of the centrum of the atlas, the neural arches, etc.

The cervical has the small hypapophysis composed of two small separated tubercles slightly prominent. The dorsal, with a prominent hypapophysis which is truncate in front and at the end, has the round cup characteristic of this species and the *H. tenebrosus*. The dermal plates are large, elongate-quadrate, considerably exceeding the frontal region in width. Their fossæ are in some deep, wider than the interspaces, in others smaller, the plate with a broad smooth bevelled border.

The cranium exhibits the specific and generic characters very well. The muzzle is broken off at the anterior extremity of the pre-frontal bone, showing that there is no foramen as in *Thoracosaurus*. The acute posterior extremities of the nasals remain. At the anterior border of the orbits the lachrymal is wider than the pre-frontal and the pre-frontal wider than the frontal.

The pre-frontal suture does not extend further back than opposite the middle point of the diameter of the orbit. No part of the orbital margins are everted, except for a shorter distance on the malar bone. The temporal or crotaphite fossae are of about the same area as the orbits. The width separating them is very little less than one-half the distance between the orbits. The anterior wall of the foramen is not quite vertical as in *H. tenebrosus*, nor very oblique as in other species. The sculpture is less marked than in the latter, and though it would become perhaps more profound with age, it is quite different in pattern from these. There are small pits near the orbital margins, and shallow grooves which incline backwards towards the median line, which is almost smooth. There are no grooves or pits on the interparietal region. In *H. obscurus* there are large deep pits all over the frontal, which is concave, and broad smooth margins and a median line of pits on the parietal bone. In the third species (figured by Leidy *Cret. Rept.* II, 8,) the pits are more numerous and the interparietal wider, and with marginal grooves. The anterior face of the crotaphite fossa is very oblique, or thickened inwards below, while it is vertical in the *H. obscurus*.

	<i>Postfrontal</i> <i>suture,</i> <i>width.</i>	<i>Frontal</i> <i>width.</i>	<i>Parietal</i> <i>width.</i>
<i>H. brevispinis</i> ,	.52	1.23	.6
<i>H. obscurus</i> ,	.8	2.	.55
<i>H. ? sp.</i> ,	.7	1.95	.68

The surfaces of the malar, postfronto-parietal and post-temporal arches are marked with distant shallow pits. The superior concealed insertion surfaces of the supraoccipital are largely exposed, and rugose.

The basioccipital, sphenoid and pterygoids are more or less exposed. The first is vertical, with latero-inferior processes directed upwards. The sphenoid has a very narrow exposure, but this is horizontal. The posterior-inner processes of the pterygoid lie closely appressed to the sphenoid and basioccipital laterally. This arrangement is much as in the living *Gavialis gangeticus*. The posterior nares are more anterior, however, and the septum not completed. Their plane is perhaps a little above that of the orifice of the eustachian tubes. The lower extremity of the basioccipital, has a well-marked posterior keel.

Measurements.

	In.
Length (median above) to apex prefrontal,	5.5
“ (axial) to front of orbit,	4.15
“ “ “ crotaphite foramen,	2.2
Width between extremities quadrata,	6.2
“ “ postfrontal angles,	2.
“ muzzle at point frontal,	3.32
Length dermal scutum,	2.3
“ cervical vertebra (to ball),	1.7
Width crotaphite foramen,	1.7

This species furnishes the generic characters. I have not been able to ascertain the non-existence of the pre-frontal foramen in the following species, but as they bear more resemblance in the cranial sculpture and in size to this species, than to *Thoracosaurus neocaesariensis*, I refer them at present to *Holops*.”

The species may provisionally be considered valid.

Holops cordatus Cope

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1869, ‘Synopsis of the Extinct Batrachia and Reptilia of North America,’ Trans. Amer. Phil. Soc., N.S., XIV, Part 1, pp. 69, 73, 74, fig. 18, Pl. IV, fig. 7.

SUBSEQUENT REFERENCES.—COPE, E. D., 1875, ‘The Vertebrata of the Cretaceous Formations of the West,’ Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, p. 253. TOULA, F., AND KAIL, J. A., 1885, ‘Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich,’ Denkschr. k. Akad. Wissensch. Wien, p. 354, (*Crocodylus cordatus*). HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 516.

ORIGINAL TYPE FIGURES.—COPE, E. D., 1869, ‘Synopsis of the Extinct Batrachia and Reptilia of North America,’ Trans. Amer. Phil. Soc., N.S., XIV, Part 1, fig. 18, Pl. IV, fig. 7 (the vertebra depicted in the latter figure is not mentioned as part of the type, being captioned “Post-median dorsal of *Holops caudatus* Cope, from Barnesboro, one-half natural size.” It probably is part of the type).

TYPE.—(Cope) “Of this species I have only two cervical, two dorsal, and three lumbar vertebræ of one individual, all in a good state of preservation.”

TYPE LOCALITY AND LEVEL.—No reference to locality is given, except in the caption referred to above “from Barnesboro.” No level is indicated, except the Cretaceous of New Jersey.

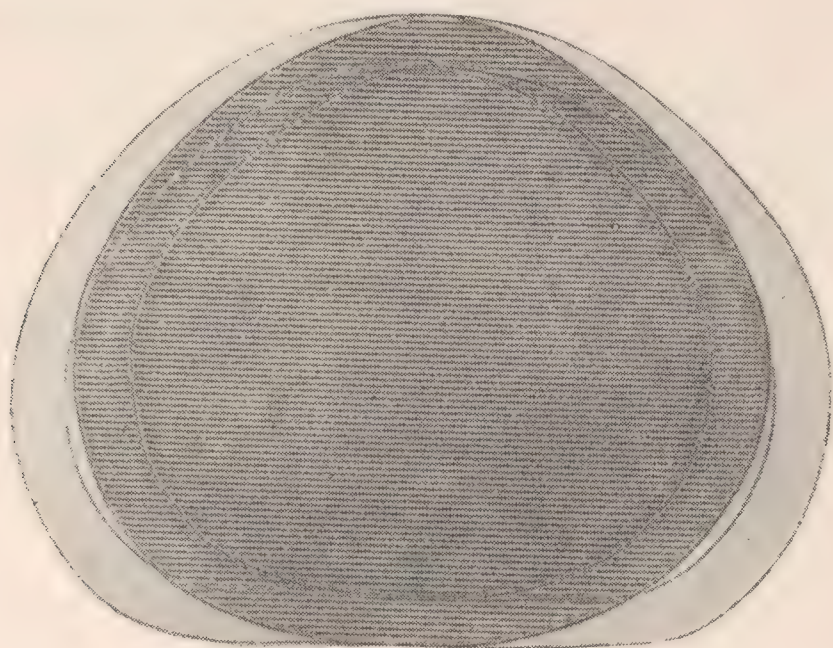


Fig. 27

Fig. 27. *Holops cordatus* Cope. Type specimen, centrum of fourth dorsal vertebra.

Size not indicated, probably natural size. The shaded portion indicates the transverse profile of a corresponding centrum of *H. basitruncatus* (Owen); the outline indicates a similar profile of *H. cordatus*. Original type figure. (After Cope.)

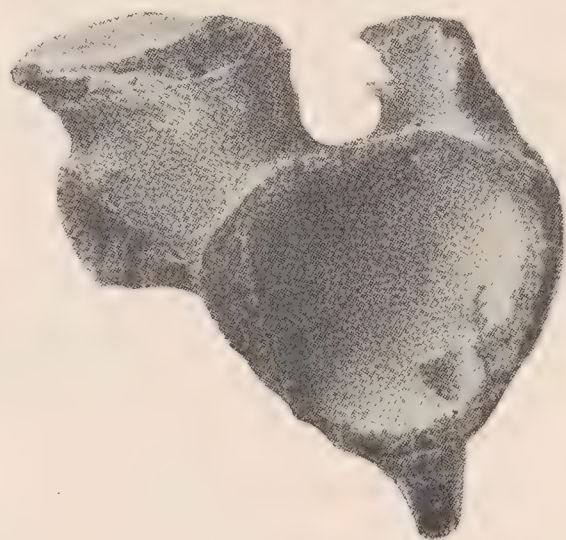


Fig. 28

Fig. 28. *Holops cordatus* Cope. Probably part of the type lot. Post-median dorsal vertebra.

One-half natural size. Anterior view. Original type figure. (After Cope.)

ORIGINAL TYPE DESCRIPTION.—“Of this species I have only two cervical, two dorsal, and three lumbar vertebræ of one individual, all in a good state of preservation. They present characters similar to those of *H. obscurus* in the cervical vertebræ, and intermediate between those of that species and the *H. tenebrosus* in the dorsals. While the fifth dorsal in the former is deeper than wide in its articular cup and slightly quadrate, the present species presents a broadly cordate cup to the fifth, narrowed below, yet considerably wider than deep; the *H. tenebrosus* presents a regularly round or transversely oval cup in the same position, much as in *H. brevispinis*. The accompanying cut exhibits the difference between this species and the *H. tenebrosus*. The cordate form is distinct on the fourth dorsal, where in *H. obscurus* the cup is regularly oval. The cervicals are not different from those of *H. obscurus*, except that the cup is rather more prolonged below, or subquadrate.

The cervical vertebræ referred to this species may be known by the outlines of the anterior extremity outside the cup, of which the latter partakes, which is between quadrate and cordate; by the distinct inferior concavity between the parapophyses, and by the gradual but complete eversion of the latter. In the types the posterior shoulder is remarkably prominent. The inferior carina is little marked on the fourth, while the hypapophyses are small and united. In a fifth, judging from the more posterior position of the parapophysis, it is formed of two partly confluent subacute elevations.

The dorsal vertebræ, from their mineralization, condition, and time and place of discovery, probably belong to the same animal as the cervicals above described. The breadth of the cup of the fifth is a little greater than the length to the posterior

shoulder, it differs from Leidy's figure of the sixth of *tenebrosus*, T. III., f. 13, in its large hypapophysis, which stands on nearly the entire centrum, and is very prominent, and concave in front; the sides of the centrum are concave from cup to shoulder. In the third dorsal but a narrow space exists behind and before the hypapophysis, and the vertical diameter of the cup is less than the transverse, and exhibits the same cordate outline. As usual some (the anterior) lumbar are deeper than wide, and in others the bodies are subquadrate in section, and the transverse diameter of the cup greater. Measurements are as follows:

	<i>In.</i>	<i>Lin.</i>
Third cervical: length to shoulder,	2	0.75
“ “ “ opposite posterior angle parapophysis,	1	4.5
“ “ width between latter points,	1	10.5
“ “ least width behind parapophysis,	1	2.
“ vertical diameter cup,	1	5.25
“ transverse diameter cup, above,	1	5.25
“ “ “ “ below,		11.
Fourth cervical: length to shoulder,	2	
“ “ “ end parapophysis,	1	2.25
Third dorsal: length to shoulder,		23.
“ “ “ opposite posterior angle parapophysis,		10.5
“ “ “ of basis of hypapophysis,		14.25
“ “ width between ends of parapophyses,		33.75
“ “ “ of neural arch just behind diapophyses,		26.
“ “ “ of anterior cup,		22.5
“ “ “ of neural arch,		5.25
“ vertical diameter neural arch,		7.5
“ “ “ cup,		19.
Fifth dorsal: length to shoulder,		21.
“ “ “ basis hypapophysis,		14.
“ “ width of centrum at middle,		12.25
“ “ “ cup,		21.25
“ “ vertical diameter at middle,		18.
Lumbar: length to shoulder,		25.5
“ vertical diameter cup,		20.
“ transverse,		19.

Portions of the frontal and parietal bones of a gavial are figured by Leidy (III., fig. 8). They are shown under the head of *H. brevispinis* not to be referable to the cranium of that species, or of *H. tenebrosus*; whether they can be referred to *H. obscurus*, *H. cordatus*, or *H. glyptodon* is as yet uncertain.

This species is no doubt a gavial-like animal, very near the *T. obscurus*. It is sufficiently different in vertebral structure; probably other differences will be found where other bones are known.”

Summary of characters on p. 68: “Large; dorsals about third and fifth, with subcordate outline and thin margins; *i.e.*, widened above, narrowed below, wider than deep; centra 20–25 lines; cervicals with subquadrate cup.”

The species may provisionally be considered valid.

Holops glyptodon Cope

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1869, 'Synopsis of the Extinct Batrachia and Reptilia of North America,' Trans. Amer. Phil. Soc., N.S., XIV, Part 1, pp. 68, 74, 231.

SUBSEQUENT REFERENCES.—COPE, E. D., 1869, 'Synopsis of the Extinct Reptilia found in the Mesozoic and Tertiary Strata of New Jersey,' in 'Geology of New Jersey,' by G. H. Cook, Appendix B, Rept. Geol. Surv. New Jersey, p. 736; 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, p. 253. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515.

ORIGINAL TYPE FIGURES.—No figures of the type have been published.

TYPE.—"This species is indicated by a few teeth only, but they are of so marked a character as to render their recognition and arrangement proper." (Cope).

TYPE LOCALITY AND LEVEL.—Barnesboro, Gloucester County, New Jersey. Cretaceous beds.

ORIGINAL TYPE DESCRIPTION.—"The best preserved specimen indicates a slender, subcylindrical strongly curved crown, with the acute ridge which divides the planes extending to its base. There are probably nine obtuse ridges on the inner or concave face, each about as wide as each interval. Both ridges and grooves are covered with sharp fine longitudinal striæ, which are continually interrupted and irregular.

The pulp cavity, as on others of the genus, is rather small. Length of crown, 12 lines; diameter at base, 4.5l. The apex is slightly compressed and smooth. In an older specimen the minute striæ are less distinct, leaving the fluting.

"From Barnesboro, Gloucester Co., N. J. Not found with or near any of the preceding specimens, but with dermal plates not distinguishable from those of *H. obscurus*."

The species may provisionally be considered valid.

Holops pneumaticus Cope

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1872, [Description of *Holops pneumaticus*], Proc. Acad. Nat. Sci. Phila., XXIV, pp. 11, 12.

SUBSEQUENT REFERENCES.—COPE, E. D., 1875, 'The Vertebrata of the Cretaceous Formations of the West,' Rept. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, II, pp. 250-252. TOULA, F., AND KAIL, J. A., 1885, 'Über einen Krokodil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich,' Denkschr. k. Akad. Wissensch. Wien, p. 354. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 516.

ORIGINAL TYPE FIGURE.—No figure of the type has previously been published. See figures 29-34 of this article.

TYPE.—Cope mentions teeth, muzzle, cervical vertebræ and long bones. Amer. Mus. Cope Coll. No. 2217.

TYPE LOCALITY AND LEVEL.—Harrisonville, New Jersey, Greensand No. 5, upper Cretaceous.

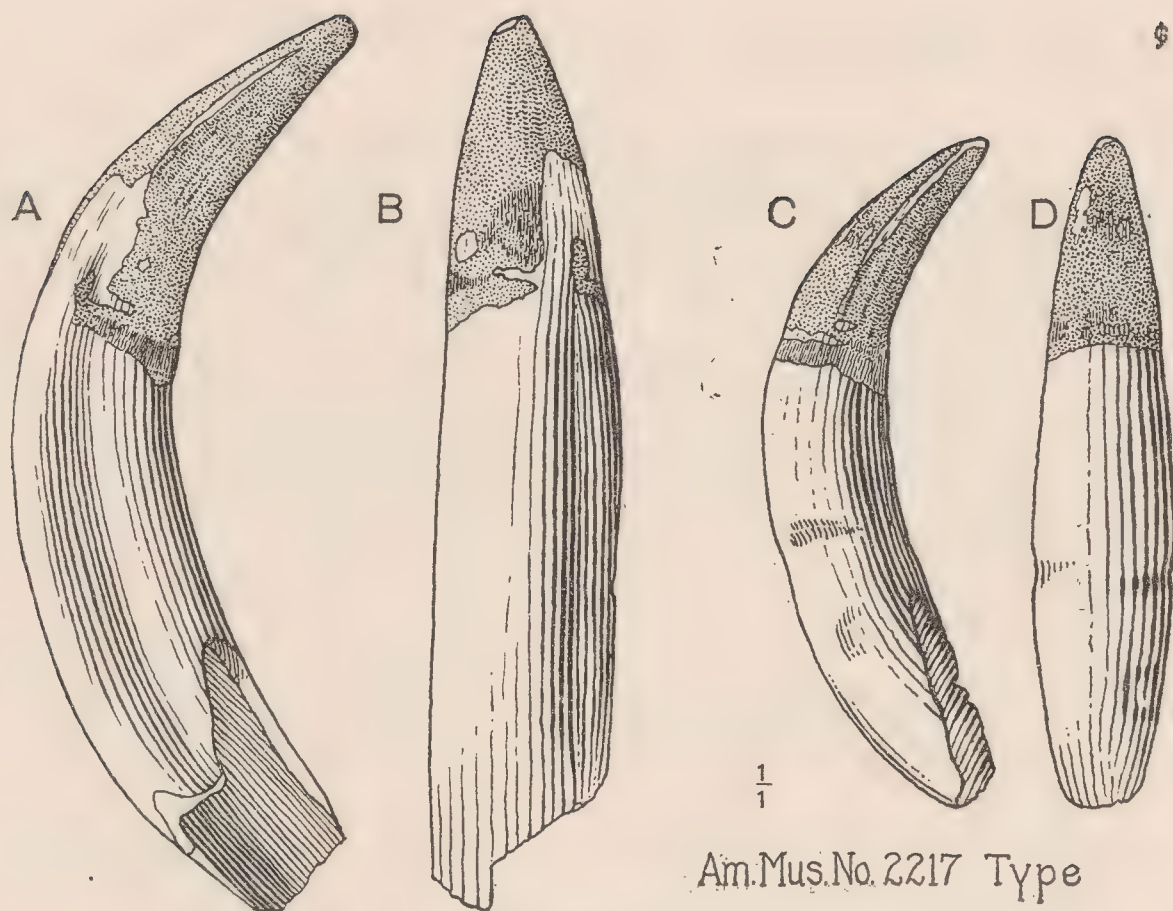


Fig. 29

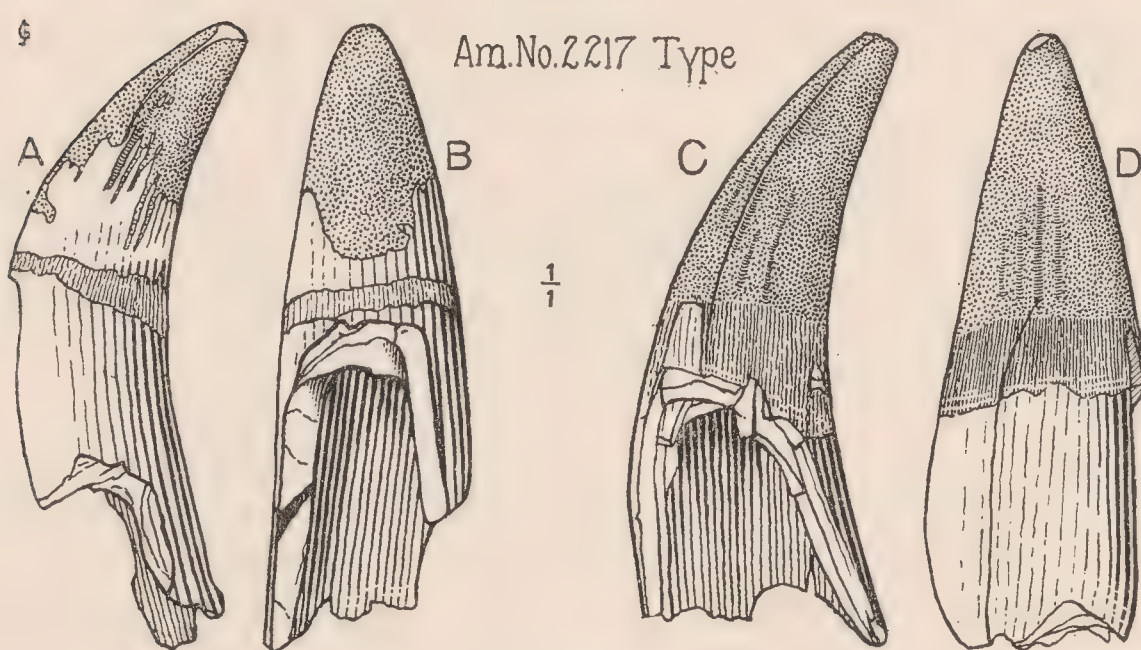


Fig. 30

Fig. 29. *Holops pneumaticus* Cope. Type specimen, teeth (Amer. Mus. Cope Coll. No. 2217).

Natural size. A, tooth, lateral view; B, the same, external view; C, another tooth, lateral view; D, the same, external view.

Fig. 30. *Holops pneumaticus* Cope. Type specimen, teeth (Amer. Mus. Cope Coll. No. 2217).

Natural size. A, tooth, lateral view; B, the same, external view; C, another tooth, lateral view; D, the same, external view.

Fig. 31. *Holops pneumaticus* Cope. Type specimen, cervical vertebra (Amer. Mus. Cope Coll. No. 2217).

One-half natural size. A, superior view; B, lateral view, right side.

Fig. 32. *Holops pneumaticus* Cope. Type specimen, anterior dorsal vertebra (Amer. Mus. Cope Coll. No. 2217).

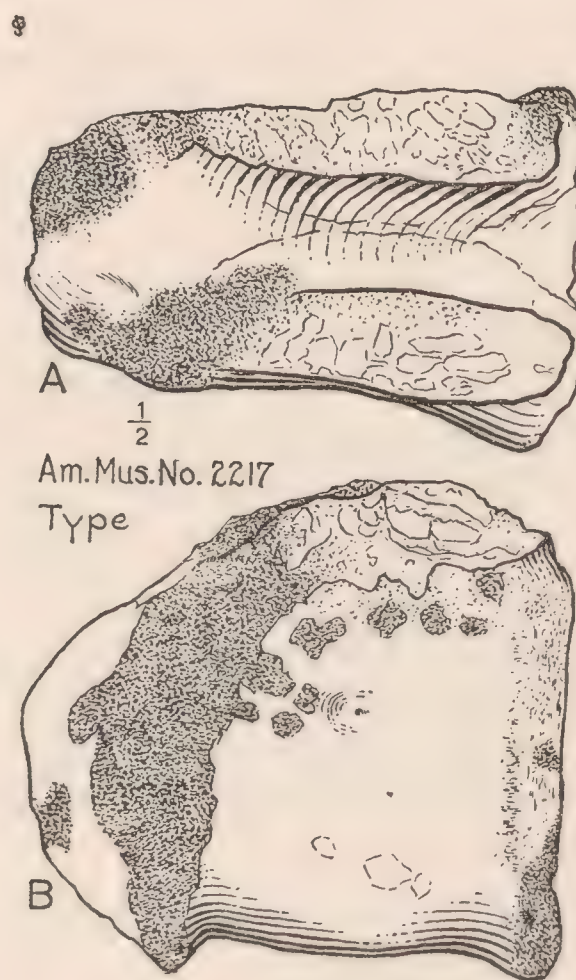
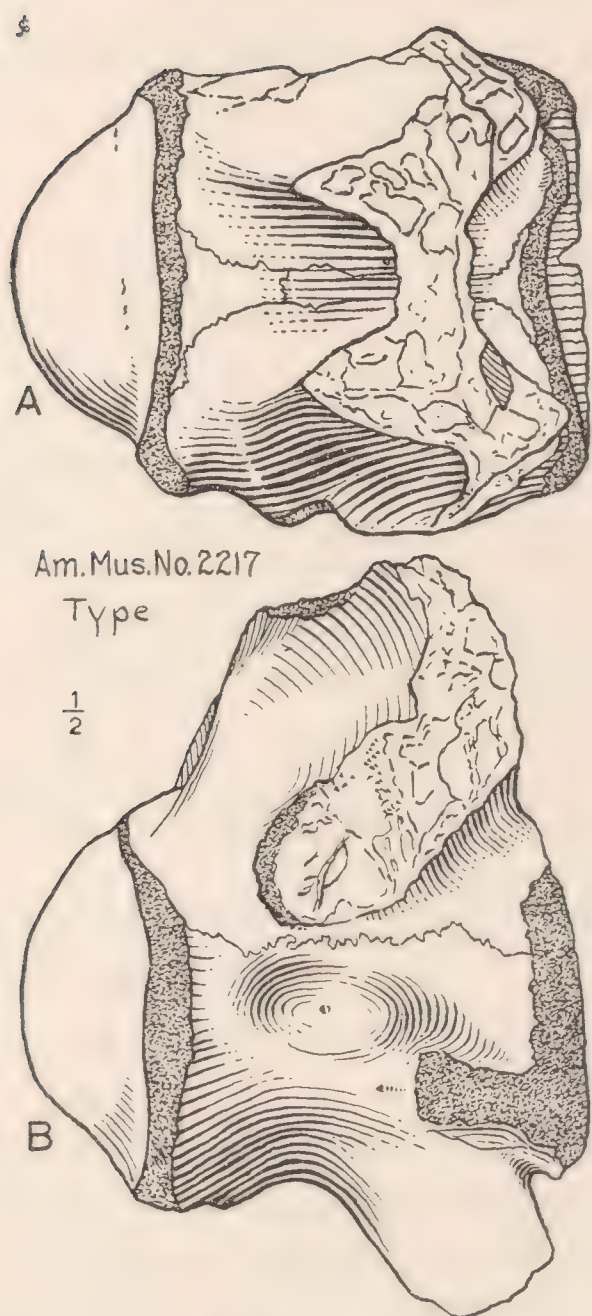
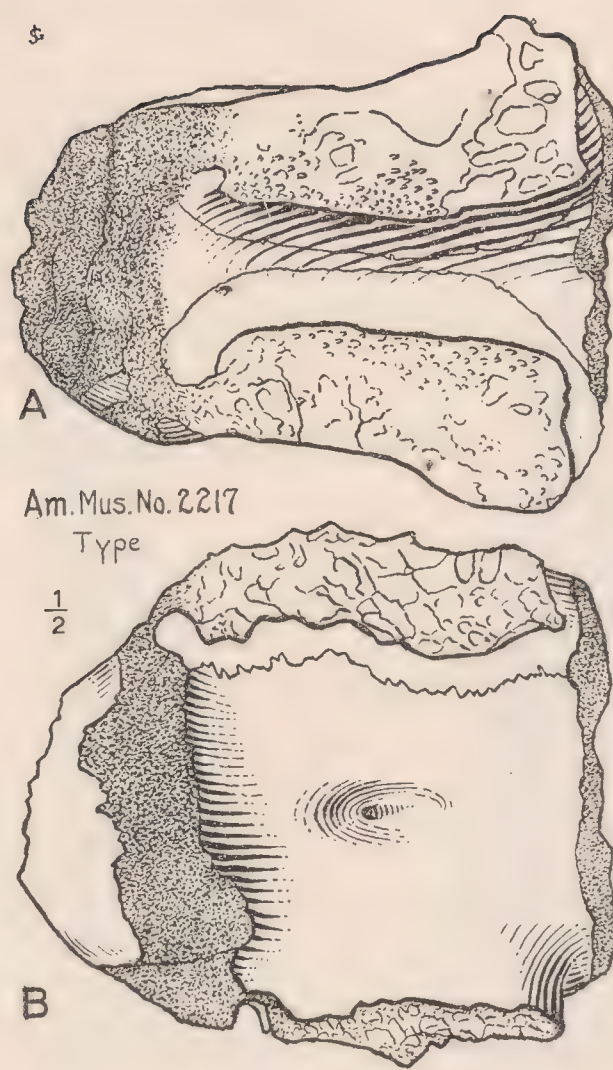
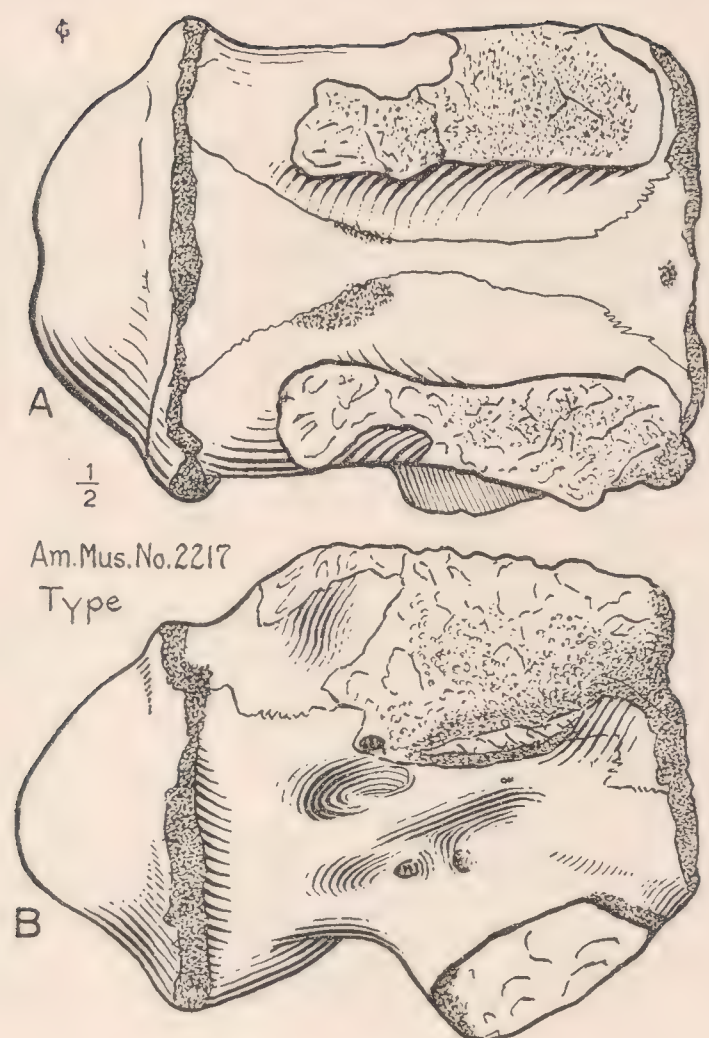
One-half natural size. A, superior view; B, lateral view, right side.

Fig. 33. *Holops pneumaticus* Cope. Type specimen, anterior dorsal vertebra (Amer. Mus. Cope Coll. No. 2217).

One-half natural size. A, superior view; B, lateral view, right side.

Fig. 34. *Holops pneumaticus* Cope. Type specimen, lumbar vertebra (Amer. Mus. Cope Coll. No. 2217).

One-half natural size. A, superior view; B, lateral view, right side.



ORIGINAL TYPE DESCRIPTION.—“Prof. Cope exhibited a portion of the skeleton of a large crocodile from the cretaceous green sand of New Jersey, belonging to the genus *Holops*. The teeth were smooth, cylindric, acute, and much curved, the muzzle gavial-like. The cervical vertebræ were very large, and of depressed form; the walls of the long bones unusually thin, and pneumatic foramina large. He called it *Holops pneumaticus*.”

The species may provisionally be considered valid.

POLYDECTES Cope

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1869, [Remarks on *Eschrichtius polyporus*, *Hypsibema crassicauda*, *Hadrosaurus tripus* and *Polydectes biturgidus*], Proc. Acad. Nat. Sci. Phila., XXI, p. 192.

SUBSEQUENT REFERENCES.—COPE, E. D., 1870, ‘On Some Reptilia of the Cretaceous Formation of the United States,’ Proc. Amer. Phil. Soc., XI, p. 271; 1875, ‘Synopsis of the Vertebrata whose Remains have been Preserved in the Formations of North Carolina,’ Rept. Geol. Surv. North Carolina, I, Appendix B, p. 34. HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 514.

TYPE.—*Polydectes biturgidus* Cope.

ORIGINAL TYPE DESCRIPTION.—Not separated from specific description of *P. biturgidus*. See the latter.

Further study is necessary to permit a reliable determination.

Polydectes biturgidus Cope

ORIGINAL TYPE REFERENCE.—1869, [Remarks on Fossil Reptiles], Proc. Acad. Nat. Sci. Phila., XXI, p. 192. (This is an abstract of a verbal communication by Prof. Cope).

SUBSEQUENT REFERENCES.—COPE, E. D., 1870, ‘On Some Reptilia of the Cretaceous Formation of the United States,’ Proc. Amer. Phil. Soc., XI, p. 271. (This is the first published account by Cope himself); 1875, ‘Synopsis of the Vertebrata whose Remains have been Preserved in the Formations of North Carolina,’ Rept. Geol. Surv. North Carolina, I, Appendix B, pp. 33, 34, Pl. VIII, figs. 2, 2a. HAY, O. P., 1902, ‘Bibliography and Catalogue of the Fossil Vertebrata of North America,’ Bull. U. S. Geol. Surv., No. 179, p. 514.

ORIGINAL TYPE FIGURES.—COPE, E. D., 1875, ‘Synopsis of the Vertebrata whose Remains have been Preserved in the Formations of North Carolina,’ Rept. Geol. Surv. North Carolina, I, Appendix B, Pl. VIII, figs. 2, 2a.

TYPE.—“an elongate conic tooth, and perhaps by others,” Geol. Surv. North Carolina Coll.

TYPE LOCALITY AND LEVEL.—Sampson County, North Carolina. In marl pits, probably Cretaceous.

ORIGINAL TYPE DESCRIPTION.—In the record of meetings of the Academy of Natural Sciences of Philadelphia the following note is given: “Another reptile from the same locality was indicated by an elongate, conic tooth, and perhaps by others, which had the cone in cone structure of those of the species of the Crocodilian genus, *Thecachampsa*. It differed from all these in the removal of the usually opposite

dividing cutting ridges to a position near together on the inner face of the crown, and the slight median contraction of the crown, which produced an appearance of enlargements a short distance above the base and below the tip of the crown. Crown conic; length 2 in., 6 lines. He named it *Polydectes biturgidus*." Cope's description of 1870 is as follows: "Crown a slender cone slightly curved near the base. Middle portion constricted, its surface marked with narrow obscure facets. On the inner face, a shallow groove within each of the bounding sulci; the two separated by an indistinct groove. The enamel is smooth and worn, and leaves no traces of other sculpture.

	Lines.
Length of crown.....	30
Diameter at base of do.....	10
" middle.....	6.
" above do.....	6.5

From the marl pits of James King, Sampson co., N. Ca. Discovered by Prof. W. C. Kerr, Director of the Geological Survey of North Carolina."

The species may provisionally be considered valid.

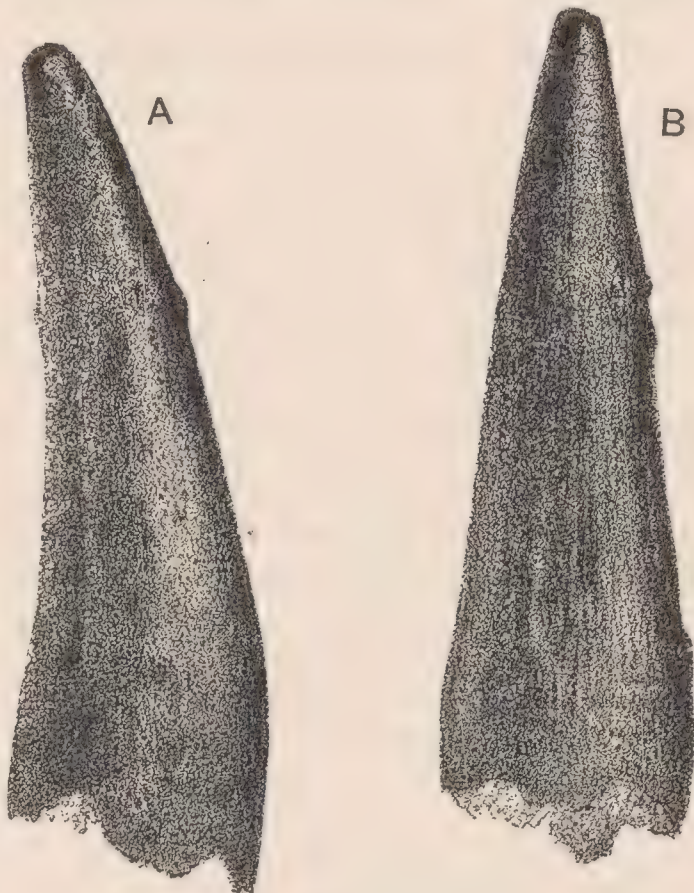


Fig. 35. *Polydectes biturgidus* Cope. Type, tooth (Geol. Surv. North Carolina Coll.).
Slightly less than natural size. A, lateral view; B, external view. Original type figures. (After Cope.)

DIPLOSAURUS Marsh

ORIGINAL TYPE REFERENCE.—MARSH, O. C., 1877, 'Notice of Some New Vertebrate Fossils,' Amer. Journ. Sci. and Arts, Ser 3, XIV, p. 254.
SUBSEQUENT REFERENCES.—MARSH, O. C., 1877, 'Introduction and Succession of Vertebrate Life in America,' Amer. Journ. Sci. and Arts, Ser. 3, XIV, Art. 42, p. 346; 1896, 'A New Belodont Reptile (Stegomus) from the Connecticut River Sandstone,' Amer. Journ. Sci., Ser. 4, II, p. 62. WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol., XIV, p. 8.

TYPE.—*Diplosaurus felix* Marsh.

ORIGINAL TYPE DESCRIPTION.—The characters of the genus were not separated from those of the type species by Marsh. See *Goniopholis* (*Diplosaurus*) *felix*.

The genus may provisionally be considered as synonymous with *Goniopholis* Owen.

AMPHICOTYLUS Cope

ORIGINAL TYPE REFERENCE.—COPE, E. D., 1878, 'Descriptions of New Extinct Vertebrates from the Upper Tertiary and Dakota Formations,' Bull. U. S. Geol. Surv. Terr., F. V. Hayden in Charge, IV, No. 2, Art. 16, p. 391.
SUBSEQUENT REFERENCES.—NICHOLSON, H. A., AND LYDEKKER, R., 1889, 'A Manual of Palæontology for the Use of Students with a General Introduction on the

Principles of Palæontology,' p. 1190. HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv. No. 179, p. 516. WILLISTON, S. W., 1906, 'American Amphicælian Crocodiles,' Journ. Geol., XIV, p. 7.

TYPE.—*Amphicotylus lucasii* Cope.

ORIGINAL TYPE DESCRIPTION.—“*Char. gen.*—The portions certainly representing this genus consist of dorsal and lumbar vertebræ, ribs, and dermal bones. These indicate that the form is to be referred to the amphicæulous division of the *Crocodylia*. The extremities of the centrum are regularly cupped, and concavity being separated from the edge of the articular face by a plane border. The neural arch is co-ossified with the centrum, which does not display any lateral fossa. It is, however, considerably compressed. The diapophysis of the dorsal is below the neural arch, and near the anterior extremity of the centrum. On the lumbar it rises from the arch, and is long and flat. The anterior zygapophysis projects but little from its anterior border, while the posterior forms a considerable process. There is no hypapophysis on any of the lumbar, and probably none on the last dorsal vertebra. The tissue of the neural canal presents a shallow excavation at the middle of the centrum, uniform and rather finely spongy.

The technical characters of this genus are somewhat like those of *Symphyrophus*, . . . but the two forms are very distinct. The vertebræ of the latter are amphiplatyan, not amphicæulous, and there is a lateral fossa.”

The genus may provisionally be considered a synonym of *Goniopholis* Owen.

HETERODONTOSUCHUS Lucas

ORIGINAL TYPE REFERENCE.—LUCAS, F. A., 1898, 'Contributions to Paleontology. 1. A New Crocodile from the Trias of Southern Utah,' Amer. Journ. Sci., Ser. 4, VI, p. 399.

SUBSEQUENT REFERENCE.—HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515.

TYPE.—*Heterodontosuchus ganei* Lucas.

ORIGINAL TYPE DESCRIPTION.—Not separated by Lucas from the description of the type species. See *Heterodontosuchus ganei*.

The genus may provisionally be considered valid.

Heterodontosuchus ganei Lucas

ORIGINAL TYPE REFERENCE.—LUCAS, F. A., 1898, 'Contributions to Paleontology. 1. A New Crocodile from the Trias of Southern Utah,' Amer. Journ. Sci., Ser. 4, VI, p. 399.

SUBSEQUENT REFERENCE.—HAY, O. P., 1902, 'Bibliography and Catalogue of the Fossil Vertebrata of North America,' Bull. U. S. Geol. Surv., No. 179, p. 515.

ORIGINAL TYPE FIGURES.—No figures of the type have been published.

TYPE.—An imperfect anterior portion of the mandible. U. S. Nat. Mus. No. 4136.

TYPE LOCALITY AND LEVEL.—Clay Hill, southern Utah. At the top of Bed No. 10 of Newberry, Triassic (?).

ORIGINAL TYPE DESCRIPTION.—“The following genus and species is based upon the imperfect anterior portion of the lower mandible of a crocodile comparable in size with *Tomistoma* among living and *Thoracosaurus* among extinct species. The mandibular symphysis is long, though less than in *Tomistoma*, and includes a considerable portion of the splenial. The teeth are very close to one another, being separated by an extremely thin partition of bone, and the tooth row lies in a broad shallow groove. The teeth are set obliquely, raking decidedly outwards, and they are compressed from before backward, the antero-posterior diameter being slightly less than the transverse. The two anterior teeth are round in section and vastly larger than the others, the end of the jaw being expanded for their accommodation. The surface of the bone is somewhat pitted, there is a deep narrow groove along the side of the jaw and there is no notch for the upper canines and no depressions for the reception of any of the upper teeth. The genus is characterized by the antero-posterior compression of the teeth, their closeness to one another, and by the great size of the two anterior teeth. The name *Heterodontosuchus ganei* is proposed for the genus and species, the specific name being given in honor of the discoverer Mr. H. S. Gane.”

The species may provisionally be considered valid.

TELEORHINUS Osborn

ORIGINAL TYPE REFERENCE.—OSBORN, H. F., 1904, ‘*Teleorhinus browni*—A Teleosaur in the Fort Benton,’ Bull. Amer. Mus. Nat. Hist., XX, Art. 21, p. 239.

SUBSEQUENT REFERENCE.—WILLISTON, S. W., 1906, ‘American Amphicœlian Crocodiles,’ Journ. Geol., XIV, pp. 5, 6.

TYPE.—*Teleorhinus browni* Osborn.

ORIGINAL TYPE DESCRIPTION.—“Cranium teleosauroid. Nasals continued forward to form roof border of anterior nares. Splenials prolonged into symphysis. Teeth compressed antero-posteriorly, uniformly grooved in front and behind.”

The genus may provisionally be considered valid.

Teleorhinus browni Osborn

ORIGINAL TYPE REFERENCE.—OSBORN, H. F., 1904, ‘*Teleorhinus browni*—A Teleosaur in the Fort Benton,’ Bull. Amer. Mus. Nat. Hist., XX, Art. 21, pp. 239, 240.

SUBSEQUENT REFERENCE.—WILLISTON, S. W., 1906, ‘American Amphicœlian Crocodiles,’ Journ. Geol., XIV, p. 6.

ORIGINAL TYPE FIGURE.—No figure of the type has previously been published. See figure 36 of this article.

TYPE.—Skull, jaws and considerable part of the skeleton. Amer. Mus. No. 5851.

TYPE LOCALITY AND LEVEL.—Thirty miles southeast of Pryor, Montana. Fort Benton Formation.

ORIGINAL TYPE DESCRIPTION.—“Forty maxillary and premaxillary teeth. Premaxillary teeth straight, maxillary teeth recurved.

The skull (1000 mm.) and jaws (996 mm.) are preserved entire, with a large number of the upper teeth. The skull in the upper view exhibits great breadth between the orbits, which are placed laterally. Large supratemporal fenestræ. Few sutures can be made out. The fronto-prefrontal elements connect anteriorly with the greatly elongated nasals which border the roof of the anterior nares.

The vertebræ are amphicœlous or amphiplatyan.

Nine *cervicals* are preserved. Atlas with hypocentrum, neurocentra (neural arches), and a single transversely extended proatlas with median spine. Axis with firmly united odontoid (pleurocentrum of atlas), with paired hypocentra indicated,

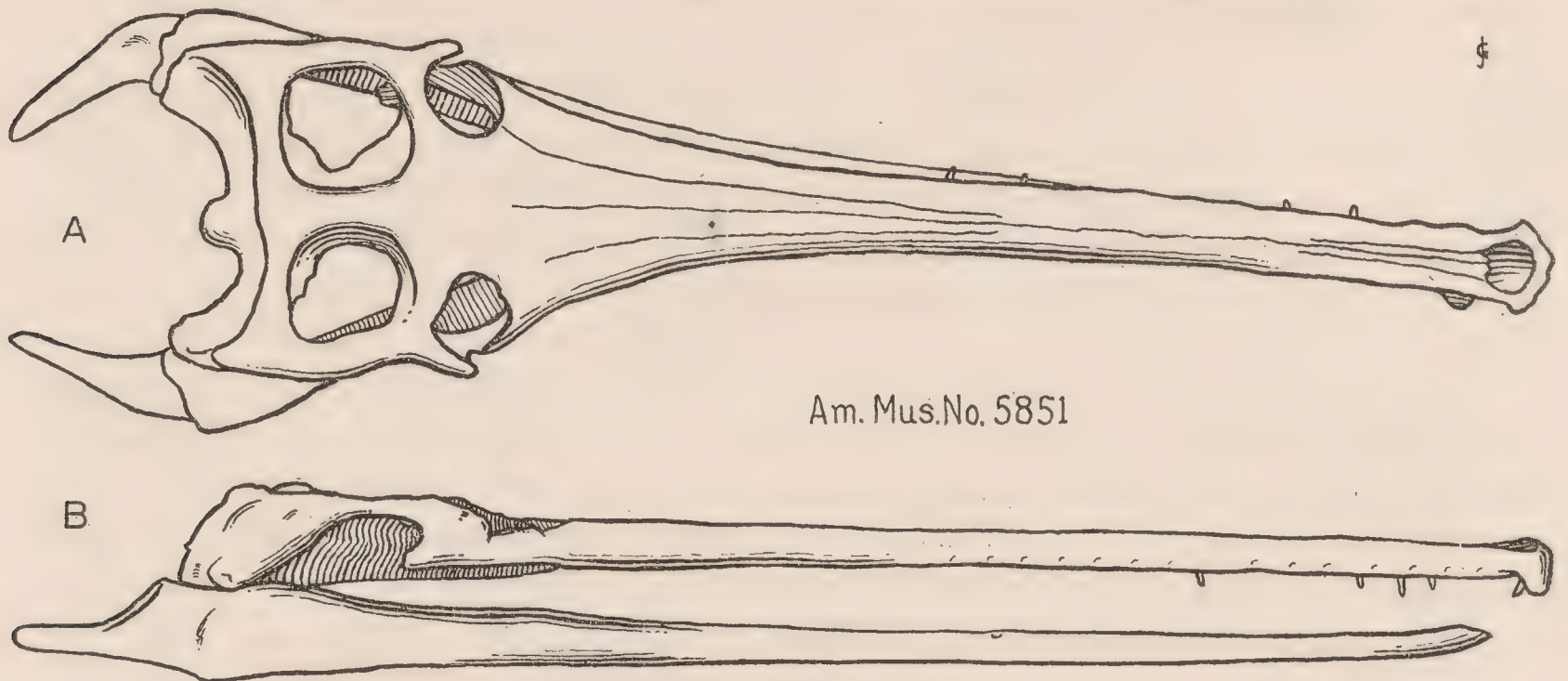


Fig. 36. *Teleorhinus browni* Osborn. Type specimen, skull and jaws (Amer. Mus. No. 5851).

One-tenth natural size. A, superior view; B, lateral view, left side.

but not osseous or preserved; with prominent and elongate spine. Remaining cervicals with very broad ribs, articulating with depressed dia- and parapophyses. At least twelve dorsal centra are preserved, without upper portion or neural spines. The single sacral preserved has a broad sacral rib attachment directly opposite the centrum; the centrum is amphiplatyan and front and back surfaces are of equal size. The mid-caudal centra are laterally compressed, with chevron facets.

Of the limb bones the femur and humerus are preserved complete. Both are much straighter than in *Hyposaurus* and greatly reduced in length. The dermal scutes are elongated and shallow-pitted."

The species may be considered valid.

COELOSUCHUS Williston

ORIGINAL TYPE REFERENCE.—WILLISTON, S. W., 1906, 'American Amphi-coelian Crocodiles,' Journ. Geol., XIV, pp. 9-12.

SUBSEQUENT REFERENCE.—No subsequent reference is available at the present time.

TYPE.—*Cælosuchus reedii* Williston.

ORIGINAL TYPE DESCRIPTION.—The generic characters are not separated from those of the type species in Williston's description. See *Cælosuchus reedii*.

The genus may provisionally be considered valid.

Coelosuchus reedii Williston

ORIGINAL TYPE REFERENCE.—WILLISTON, S. W., 1906, 'American Amphi-coelian Crocodiles,' Journ. Geol. XIV, pp. 9-12, figs. 1-12.

SUBSEQUENT REFERENCES.—None.

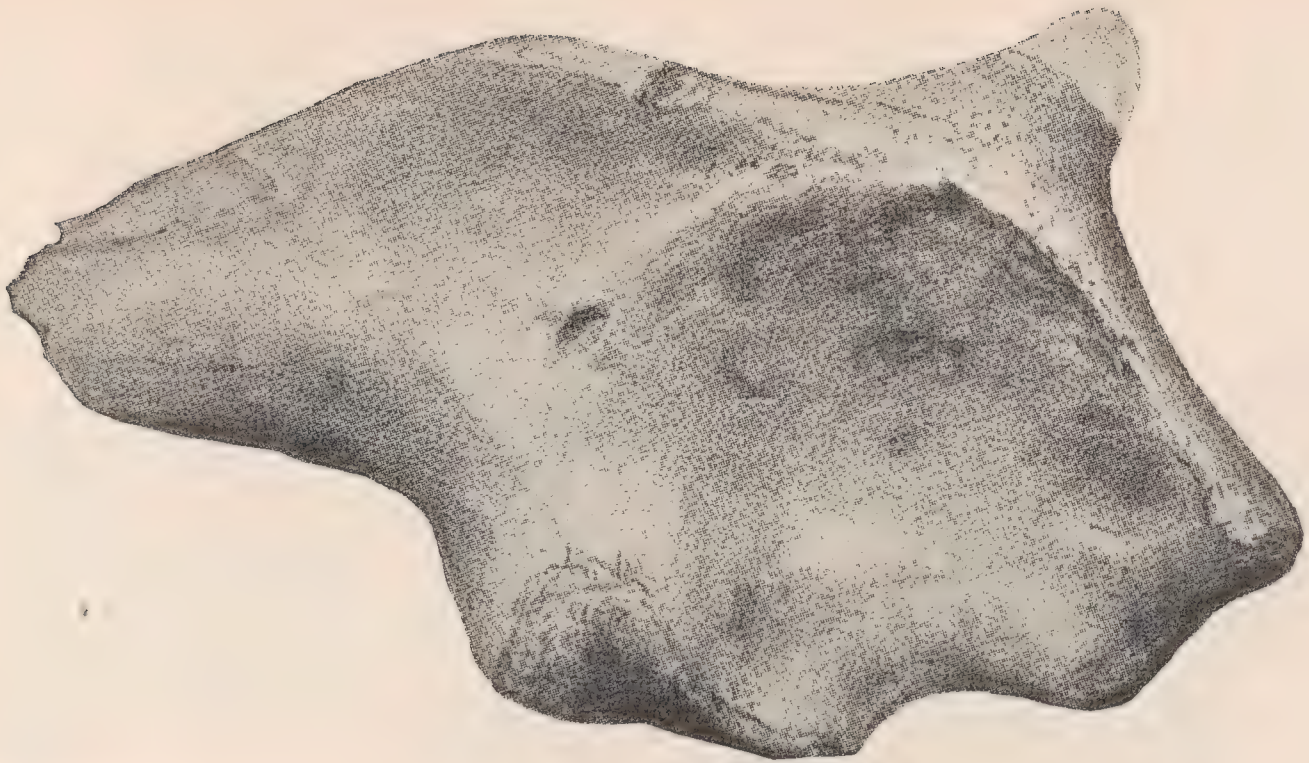


Fig. 37



Fig. 38

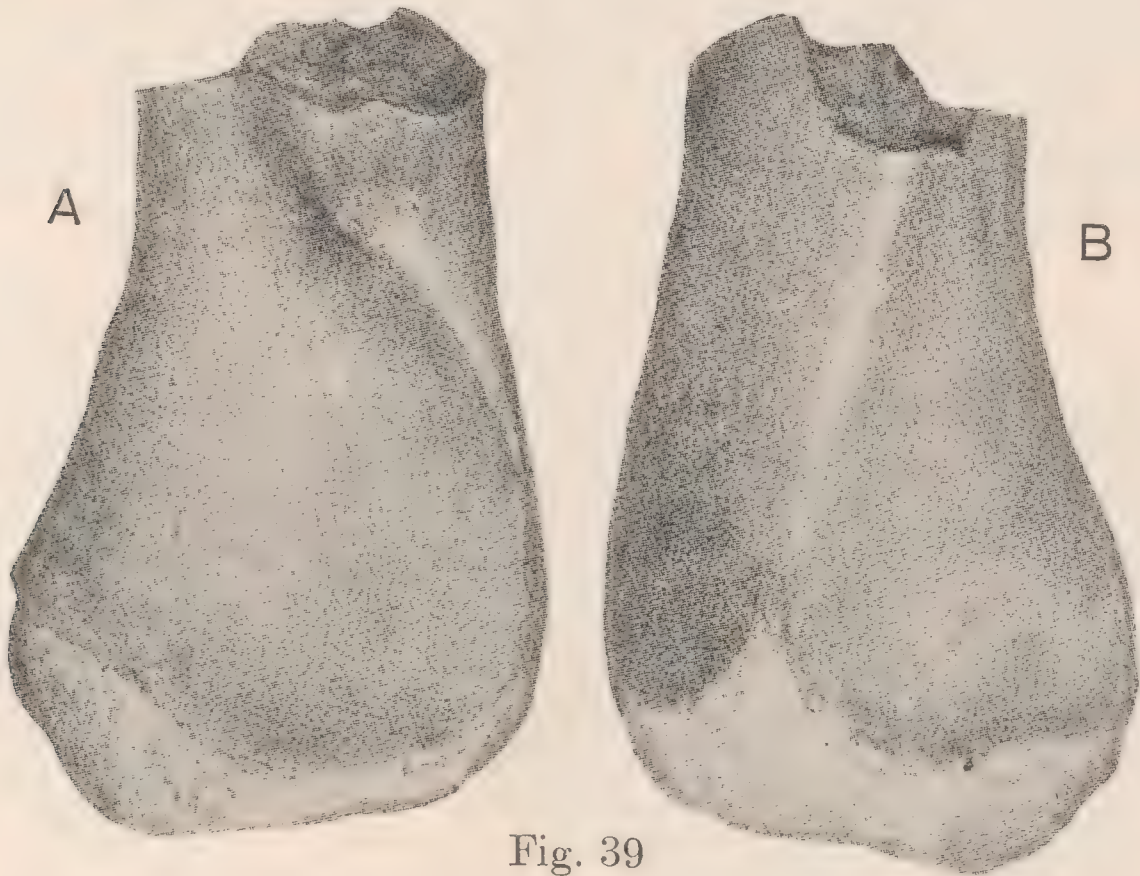


Fig. 39

Fig. 37. *Cælosuchus reedii* Williston. Cotype specimen, right ilium (Mus. Univ. Wyo. Coll.).

One-half natural size. External view. Original type figure. (After Williston.)

Fig. 38. *Cælosuchus reedii* Williston. Cotype specimen, right pubis (Mus. Univ. Wyo. Coll.).

One-half natural size. Original type figure. (After Williston.)

Fig. 39. *Cælosuchus reedii* Williston. Cotype specimen, proximal end of humerus (Mus. Univ. Wyo. Coll.).

One-half natural size. A, posterior view; B, anterior view. Original type figures. (After Williston.)



Fig. 40. *Caelosuchus reedii* Williston. Cotype specimen, right coracoid (Mus. Univ. Wyo. Coll.)
One-half natural size. External view. Original type figure. (After Williston.)



Fig. 41. *Caelosuchus reedii* Williston. Cotype specimens (Mus. Univ. Wyo. Coll.).

Two-thirds natural size. A, left ischium, internal view; B, left tibia, distal end, external view; C, the same, distal view; D, centrum of cervical vertebra, anterior view; E, centrum of dorsal vertebra, anterior view; F, caudal vertebra, lateral view, left side. G, another caudal vertebra, posterior view. Original type figures. (After Williston.)

ORIGINAL TYPE FIGURES.—WILLISTON, S. W., 1906, 'American Amphicoelian Crocodiles,' Journ. Geol. XIV, figs. 1-12.

COTYPES.—"Remains of a large amphicoelian crocodile, evidently of a brachystomous form." Ilium, ischium, pubes of several individuals, humerus, tibia, coracoids, vertebræ, fragments of skull. Mus. Univ. Wyo.

TYPE LOCALITY AND LEVEL.—"In the vicinity of Wilcox, Wyo., in a dark shale of the Graneros division of the Benton, and below the heavily laminated shales which must be ascribed to the Mowrie beds of Darton."

ORIGINAL TYPE DESCRIPTION.—"The ilium (Fig. 1) differs from that of a modern crocodile in the greater elongation of the posterior process, and in the relatively less width of the bone. An ischium (Fig. 5) of a smaller individual differs in the less expansion of the distal end, its more rounded posterior angle, and the greater obliquity of the shaft of the bone. The pubes of several individuals are represented by more or less fragmentary parts, all of about one size. One nearly complete specimen is shown in Fig. 2. It is also noticeable for the slenderness of the shaft, and the moderate dilatation of the distal extremity, differing markedly in this respect from the known forms of *Goniopholis* and *Bernissartia*. The upper extremity of a humerus of a large individual is shown in Fig. 3. Its curvature is slight, much less than of a humerus of nearly equal size of a longirostrate form from the Hailey shales. Other smaller humeri are present, nearly complete. They are slender and nearly straight, the lower extremity scarcely differing from that of a modern alligator or crocodile. The distal end of a tibia and its distal face are shown in Figs. 6 and 7. The proximal and distal ends of two large coracoids are shown in the figure. I have outlined the connecting part between them as would seem natural. The distal extremity is also noticeable for its moderate expansion.

The numerous vertebræ preserved are of various sizes and from various places in the vertebral column. A cervical (Fig. 8) has its extremities almost amphiplatyan: the hypapophysis is small; the parapophysial articulations are not large and are situated near the end. The neurapophyses are attached by a loose suture. The length of the vertebra is 50 mm.; its width, 44 mm. A dorsal centrum, of which the anterior articular surface is shown in Fig. 9, has a very smooth surface exteriorly, and is but gently concave longitudinally. The posterior central articular surface is nearly flat, the anterior rather deeply cupped. The length of the centrum is 59 mm; its width, 50 mm. Another centrum (Fig. 10) is much more compressed from side to side, presenting a vertically oval figure at the ends and in cross-section. This centrum has a length of 50 mm and a width of but 36 mm. The largest (dorsal) centrum preserved has a length of 65 mm and a width of 70 mm.

Various fragments of the skull are preserved, but no teeth can be detected, though a fragment of a dentary or maxilla has numerous thecæ for their reception. The skull fragments are massive and deeply pitted, conclusively proving, it seems to me, the brachystomous nature of the face. The largest portion preserved is that figured herewith, the posterior part of the left mandible. It measures 155 mm, in its greatest width, and resembles the corresponding part of the mandible of *Goniopholis tenuidens*, as figured by Owen. . . . If the skulls of the two species were of like proportions, the present must have measured over four feet in length. Species of *Goniopholis* have no mandibular foramen, so characteristic of the crocodiles, and its absence in the present species, together with the great width of the bone and its numerous deep pittings, indicates conclusively the brevirostrate character of the form. This is also indicated

by the large size of the anterior extremities, the bones preserved showing that they were fully as large as the posterior ones, a character also seen in *Goniopholis* and *Bernissartia*, and very different from the small fore legs of the longirostrate types."

The species may be considered valid.

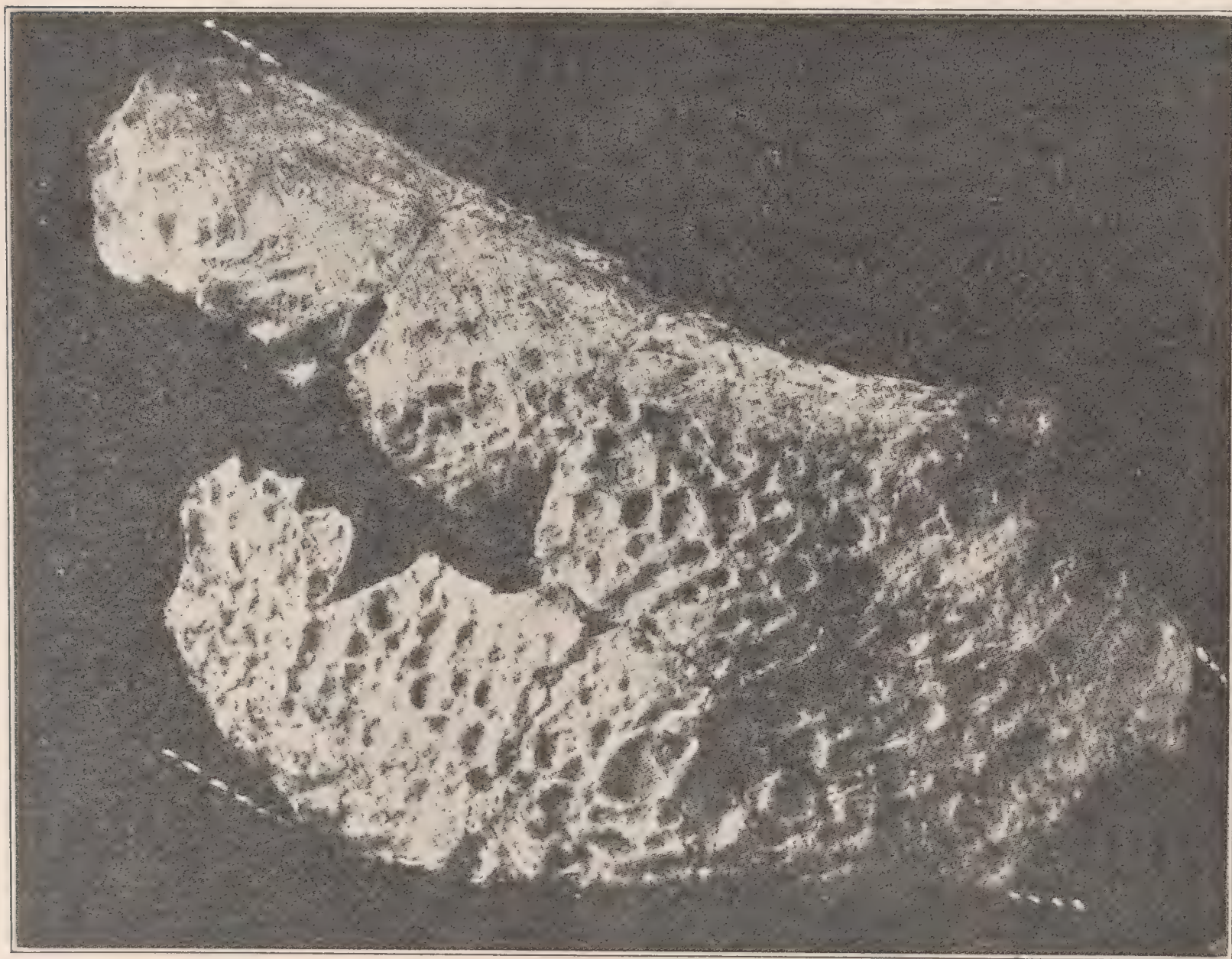


Fig. 42. *Caelosuchus reedii* Williston. Cotype specimen, posterior portion of left mandibular ramus (Mus. Univ. Wyo. Coll.).

One-eighth natural size. External view. Original type figure. (After Williston.)

LEIDYOSUCHUS Lambe

ORIGINAL TYPE REFERENCE.—LAMBE, L. M., 1908, 'On a New Crocodilian Genus and Species from the Judith River Formation of Alberta,' Trans. Roy. Soc. Canada, Ser. 3, I, p. 221.

SUBSEQUENT REFERENCE.—GILMORE, C. W., 1910, 'Leidyosuchus sternbergii, a New Species of Crocodile from the Ceratops Beds of Wyoming,' Proc. U. S. Nat. Mus., XXXVIII, pp. 485–501 (Pub. No. 1762).

TYPE.—*Leidyosuchus canadense* Lambe.

ORIGINAL TYPE DESCRIPTION.—The characters of the genus were not separated from those of the type species by Lambe. See *Leidyosuchus canadensis*.

The genus may be considered valid.

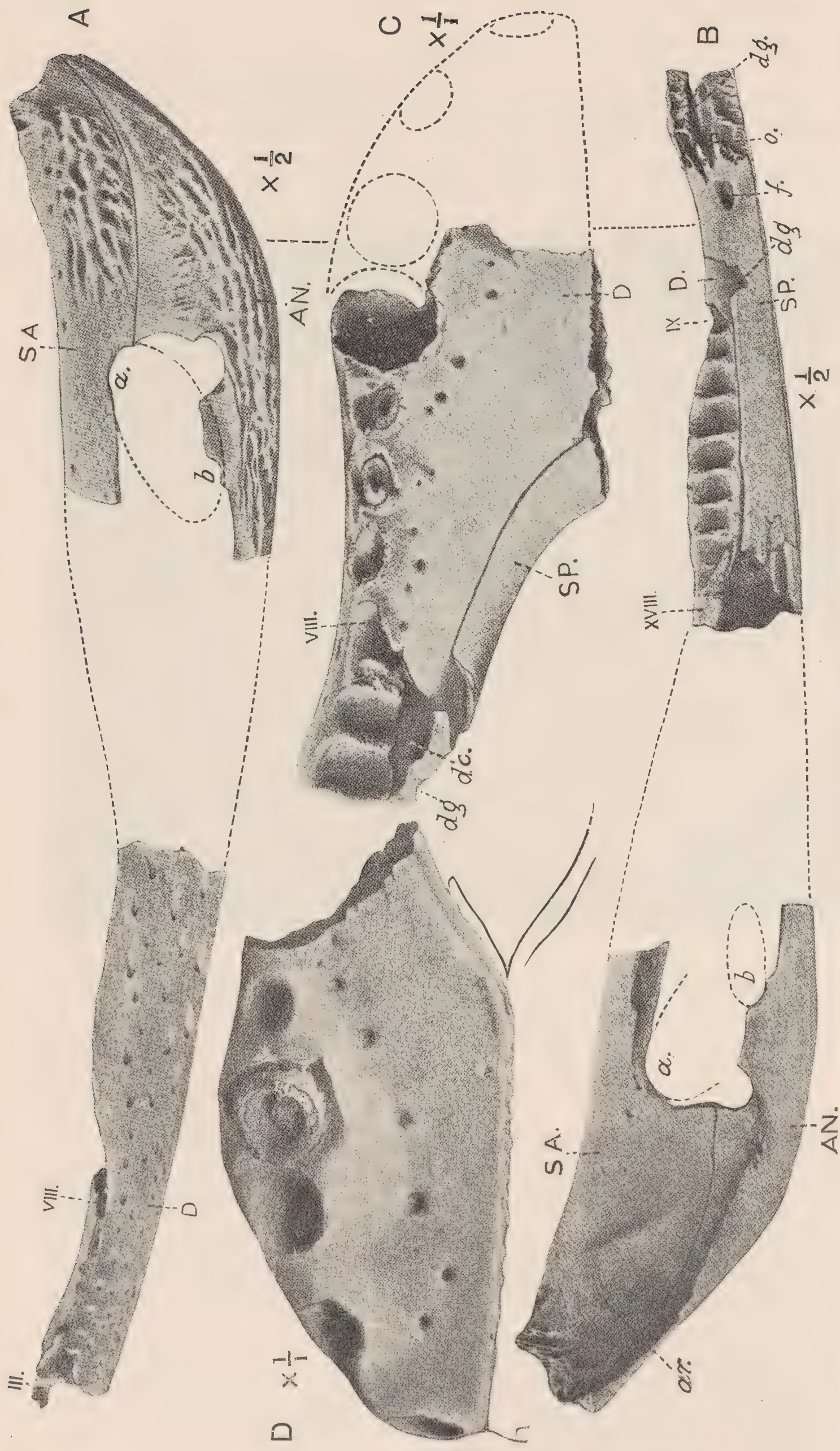


Fig. 43. *Leidyosuchus canadensis* Lambe. Type and paratype specimens; A, B, C, type, left ramus of mandible (Mus. Geol. Surv. Canada No. 338); D, paratype specimen, part of right dentary bone (Mus. Geol. Surv. Canada No. 808).

A, B, one-half natural size; C, D, natural size. A, external view of same; B, internal view of same; C, sutural surface of the articular; D, superior view of paratype; AN, angular; D, dentary; SA, surangular; sp, splenial; ar., external mandibular foramen; a., sutural surface for the articular; b, internal mandibular foramen; III., VIII., IX., XVIII., alveoli for the third, eighth, ninth and eighteenth teeth respectively; dg., dental canal; dg., dentary groove; f, postsymphysial foramen; o., opening in suture between splenial and dentary for passage of dentary groove. Original type figures. (After Lambe.)

Leidyosuchus canadensis Lambe

ORIGINAL TYPE REFERENCE.—LAMBE, L. M., 1908, 'On a New Crocodilian Genus and Species from the Judith River Formation of Alberta,' Trans. Roy. Soc. Canada, Ser. 3, I, pp. 219-244, Pls. I-V.

SUBSEQUENT REFERENCE.—GILMORE, C. W., 1910, 'Leidyosuchus sternbergii, a New Species of Crocodile from the Ceratops Beds of Wyoming,' Proc. U. S. Nat. Mus., XXXVIII, pp. 485-500 (Pub. No. 1762).

ORIGINAL TYPE FIGURES.—LAMBE, L. M., 1908, 'On a New Crocodilian Genus and Species from the Judith River Formation of Alberta,' Trans. Roy. Soc. Canada, Ser. 3, I, Pls. I-V.

TYPES.—Type: the greater part of a left mandibular ramus, Mus. Geol. Surv. Canada No. 338; paratypes: the posterior portion of a cranium, Mus. Geol. Surv. Canada No. 1551; anterior end of a right dentary bone, Mus. Geol. Surv. Canada No. 808; parts of separate dentary bones showing the alveoli for the fifth to twelfth, third to ninth, and first to ninth teeth respectively, Mus. Geol. Surv. Canada Nos. 780, 1141, 1775a; parts of three angulars, Mus. Geol. Surv. Canada Nos. 1339, 1498 and 1702; jugals, Mus. Geol. Surv. Canada Nos. 250, 781, 1006, and 1627; separate frontal bone, Mus. Geol. Surv. Canada No. 1404; right squamosal, an anterior half and a posterior half, apparently parts of the same specimen, Mus. Geol. Surv. Canada Nos. 1765 and 782i; anterior end of a right maxilla, Mus. Geol. Surv. Canada No. 783; cervical, dorsal, sacral and caudal vertebræ; numerous separate teeth; numerous scutes, Mus. Geol. Surv. Canada.

TYPE LOCALITY AND LEVEL.—Red Deer River, Alberta, below the mouth of Berry Creek, Judith River beds.

ORIGINAL TYPE DESCRIPTION.—"The following characters are revealed by the above mentioned specimens:—

1. Mandibular symphysis short, contributed to by the splenial to the extent of about one-fifth of the total symphysial length.
2. Alveolar border of mandible undulating.
3. Teeth of unequal size, conical, slightly curved, almost smooth, with an inner area defined by carinæ, the third lower attaining nearly to the size of the enlarged fourth; apparently eighteen in each ramus.
4. An external mandibular foramen, as well as a smaller internal one, present.
5. A post symphysial foramen in the splenial.
6. Orbits confluent with the lateral temporal fossæ and larger than the supra-temporal vacuities.
7. Eustachian canals enclosed.
8. The snout, as indicated by the anterior end of a maxilla, short and broad.
9. Fourth lower tooth received into a notch in the maxilla.
10. Pits of the sculptured bones of the head, and of the scutes, deep and separated by narrow ridges.
11. Vertebræ of the procoelian type.

These characters indicate a form of Eusuchia (procoelian type of vertebra) with a short snout, that differs entirely from the described brevirostrate forms in the entry of the splenial into the formation of the symphysis, a character claimed for the longirostrate forms of the suborder. A resemblance to *Diplocynodon*, Pomel, from the Lower Tertiaries of Europe is seen in the enlargement of both the third and fourth

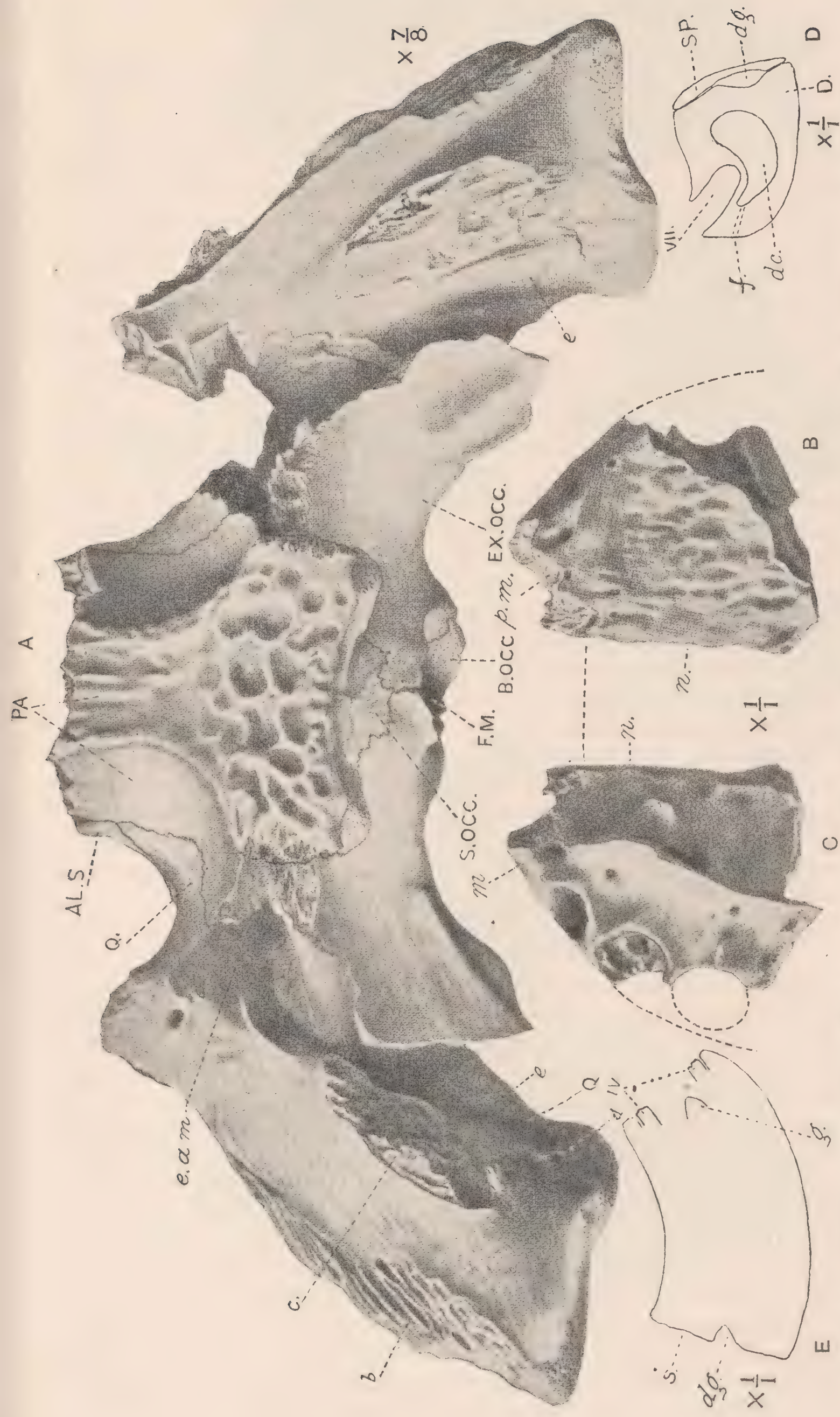


Fig. 45. *Leidyosuchus canadensis* Lambe. Type and paratype specimens, posterior portion of cranium (Mus. Geol. Surv. Canada No. 1551), seven-eighths natural size; anterior end of right maxillary (Mus. Geol. Surv. Canada No. 783), natural size; sections of mandibles, type and paratype specimens (Mus. Geol. Surv. Canada Nos. 338, 808), natural size.

A, posterior portion of cranium, superior view; B, right premaxillary, superior view; C, the same, inferior view; D, section through type mandible; E, section of paratype dentary; AL.S., alisphenoid; B.OCC., basioccipital; EX.OCC., exoccipital; F.M., foramen magnum; Q., quadrate; S.OCC., supraoccipital; SP., splenial; b, suture for quadrato-jugal; e.a.m., external auditory meatus; f., foramen; dg., dentary groove; dc., dental canal; dg., dentary groove; e.a.m., external auditory meatus; f., foramen; g., germ tooth; m., notch for fourth mandibular tooth; n., suture for nasal; p.m., suture for premaxillary; s., symphyseal surface of dentary; iv, fourth tooth; vii, alveolus for seventh tooth. Original type figures. (After Lambe.)

lower teeth (as shown by the alveoli). As a general rule in alligators the fourth lower tooth fits into a pit in the upper jaw, and in crocodiles into a marginal notch. There are exceptions to the rule, however, in each case. In *Diplocynodon*, a genus generally referred to the Alligatoridæ (of Zittel's classification), the fourth lower tooth may be received into either a pit or a notch. In the anterior end of the right maxilla from Red Deer river, a decided notch, next to the suture for the premaxilla, is preserved.

The species from Alberta may then be considered as a brevirostrate type of *Eusuchia* with resemblances to *Diplocynodon* but with a mandibular symphysis though short yet including the splenial as in some forms of the *Goniopholidæ* (*Goniopholis*, Owen): As it differs from any described species the name *canadensis* is considered appropriate and as its characters prohibit its being assigned to any known genus *Leidyosuchus* is proposed as a generic term. The writer has pleasure in associating the name of the celebrated palæontologist with this genus, particularly as Dr. Leidy was the first to record the occurrence of crocodilian remains in the Judith River formation in Montana.

Leidyosuchus occupies an anomalous position in the procelian group of the Crocodilia. It is apparently a broadnosed form and its dentition suggests an affinity to *Diplocynodon*. The entry, however, of the splenial into the formation of the symphysis is an unexpected character here and one that has been considered, among the *Eusuchia*, as belonging to the longirostrate forms (*Tomistoma*, *Gavialis*, etc.).

The question arises—may not this species from Alberta be a direct descendant of one of the brevirostrate forms of the amphiœlian *Goniopholidæ*, (*Purbeckian* and *Wealden*), having adopted a proœlian type of vertebra but still retaining the splenial in the symphysis. In the genus *Goniopholis* for instance the splenial enters the symphysis to a slight extent, also the teeth are longitudinally grooved, a resemblance indicated by the very faint fluting of the teeth of *Leidyosuchus*. In this connection it is interesting to note that the Judith River (Belly River) fauna harks back in a number of instances to Jurassic forms. It includes turtles of the Jurassic family *Pleurosternidæ*, *Plesiosaurs* and specialized *Stegosaurs*; a species of *Ornithomimus* (*O. altus*) is probably a successor to the Upper Jurassic *Ornitholestes*.

MANDIBLE OF LEIDYOSUCHUS.

The parts of the lower jaw, found together, consist of two pieces from the front and back halves of the left ramus almost completing its length (plate I, figs. 1, 1a, 1b). A portion at mid-length (restored in the figure) consisting principally of the posterior ends of the dentary and splenial bones, was not recovered. The specimen lacks the articular and coronoid elements, and the anterior end of the dentary, in advance of the alveolus for the third tooth, is missing. The alveoli of the third and succeeding fifteen teeth are preserved and it is possible that another tooth or perhaps two may have occurred posterior to the eighteenth behind which the fracture in the specimen occurs. Judging from the alveoli the fourth tooth was the largest, the third was nearly if not quite the size of the fourth, the fifth to the tenth were small and of nearly equal size, the eleventh, twelfth and thirteenth were slightly and about equally enlarged, posterior to the thirteenth the teeth gradually decreased in size to the eighteenth which was of about the size of those immediately behind the fourth. The bases of the fourth, fifth and sixth teeth are preserved in their sockets. The alveoli are complete apparently to and including the ninth, beyond this the bony divisions separating them are gradually less developed and take the form of ridges,

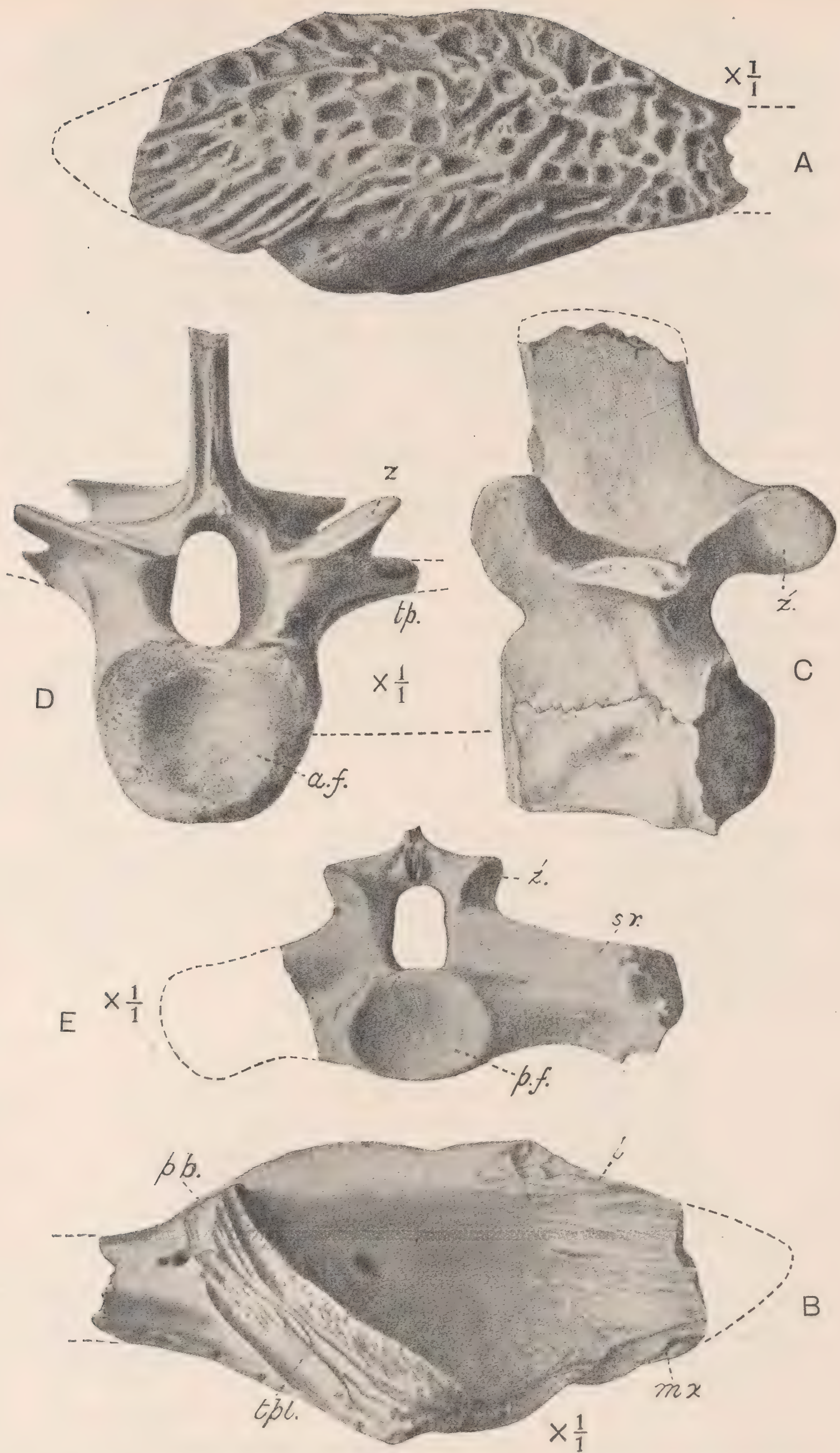


Fig. 46. *Leidyosuchus canadensis* Lambe. Paratype specimens, left jugal (Mus. Geol. Surv. Canada No. 1627); dorsal and sacral vertebræ (Mus. Geol. Surv. Canada Coll.).

Natural size. A, jugal, external view; B, the same, internal view; C, dorsal vertebra, lateral view, left side; D, the same, anterior view; E, second sacral vertebra, posterior view; *a.f.*, anterior surface of centrum; *l.*, suture for lachrymal; *mx*, suture for maxillary; *pb.*, base of postorbital bar; *p.f.*, posterior face of centrum; *sr.*, sacral rib; *tp.*, transverse process; *tpl.*, suture for ectopterygoid; *z*, prezygapophysis; *z'*, postzygapophysis. Original type figures. (After Lambe.)

on the inner side of the outer wall of the dentary. These ridges decrease in prominence backward until, between the last three teeth, there is only a slight indication of separate sockets, an evidence probably of immaturity in the individual.

Viewing the mandible from the side the outline of the dentary below, in advance of the anterior end of the angular, is straight and horizontal to the slight upturn of the extremity beneath the alveolus for the first tooth, the exact form anteriorly being given by the specimen shown in plate I, fig. 2 and by a smaller specimen (cat. No. 1775a) not figured. The alveolar border above is broadly undulating in curves that are more pronounced than in the living alligator (*Caiman latirostris*). The dentary is constricted in the neighborhood of the eighth tooth; in advance of this it expands horizontally inward and outward, attaining its greatest anterior breadth in line with the centre of the fourth tooth; posterior to the constriction the alveolar border rises in a broad convex curve to the position of the twelfth tooth adding considerably to the depth of the dentary whose upper border then continues, parallel to the inferior surface, in an almost horizontal line to the eighteenth tooth. The front teeth, the first to the fourth, were directed obliquely outward, the first and second particularly so, the other teeth had a decided inclination outward up to about the twelfth, back of which a more upright position was assumed. The reader's attention is drawn to a similar outward inclination of the front teeth of the mandible of *Diplocynodon gracile*,¹ Vaillant, from the Lower Miocene of St. Gérard le Puy (Allier) France.

The mandibular symphysis is short and contributed to by the dentary and splenial together, its posterior end being in line with the hinder edge of the alveolus for the sixth tooth. The splenial enters into the formation of the symphysis to the extent of about one-fifth of the latter's length.

A groove (Meckel's), enclosed outwardly by the splenial, channels the inner surface of the dentary at its mid-height, (*dg*, plate I, figs. 1*a*, 1*b*, and plate III, figs. 1*c* and 2*a*). It passes, in its more anterior course, from beneath the splenial forward along the symphyseal surface as far as a point opposite the division between the third and fourth teeth. The exit of the dentary groove from under the splenial is made through a transversely oval orifice (3.5 mm. wide and 2 mm. high) at the anterior end of this bone in the suture between it and the dentary (*o*, plate I, fig. 1*a*). The opening is bounded principally by the splenial, the groove in the dentary being here shallow. Thus, anterior to the two splenial elements of the mandible, the dentary grooves of the rami meet and are continued forward in the symphyseal surface as a tubular channel between the dentary bones with its termination at about the mid-length of the symphysis. The symphyseal surface of the splenial is rugose, that of the dentary is comparatively smooth. Behind the symphysis, the splenial, which is here thin with a convex outer surface, is pierced by a longitudinally elongated foramen (*f*, plate I, fig. 1*a*) that opens into the Meckelian groove. On removing the splenial a small foramen is seen in the dentary, beneath the opening in the splenial and at the lower edge of the groove, leading into the dental canal (*dc*, plate I, fig. 1*b* and plate III, fig. 1*c*). This canal passes forward, from the large cavity in the posterior half of the ramus, longitudinally through the dentary beneath the alveoli for the teeth. The splenial is applied closely to the dentary above and below the dentary groove. Mr. C. W. Gilmore in his able work on the 'Osteology of *Baptanodon*² (Marsh)' refers to a similarly placed opening in the splenial of *B. discus* from the Jurassic of Wyoming.

¹Ann. Sci. Géol. vol. III, art. 1, p. 18 (1872).'

²Memoirs of the Carnegie Museum, Pittsburgh, Vol. I, No. 2, 1905.'

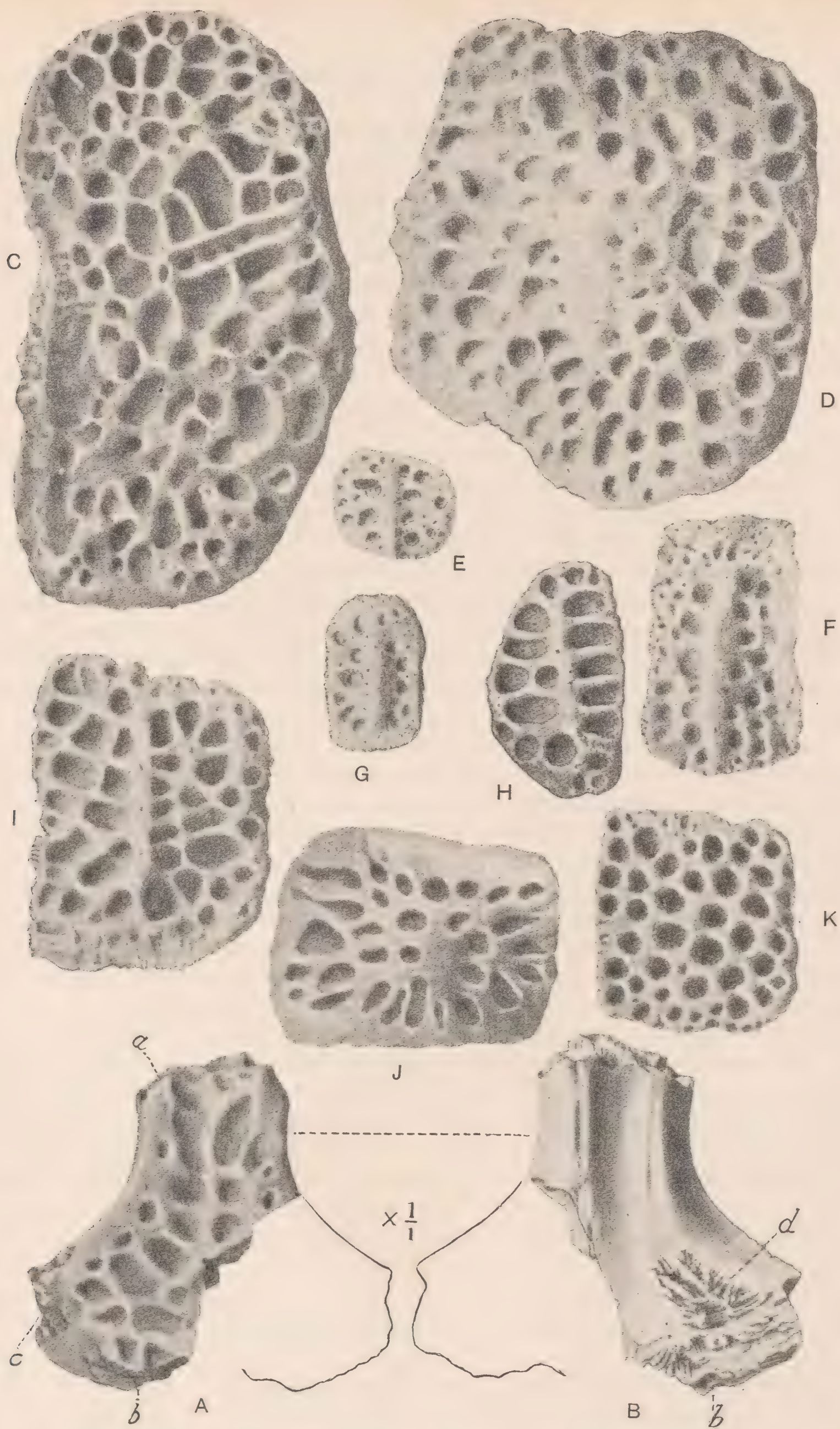


Fig. 47. *Leidyosuchus canadensis* Lambe. Paratype specimens, frontal bone (Mus. Geol. Surv. Canada No. 1404); and scutes (Mus. Geol. Surv. Canada Coll.).

Natural size. A, frontal, superior view; B, the same, inferior view; C-K, scutes, dorsal views; *a*, suture for prefrontal; *b*, suture for parietal; *c*, suture for postorbital; *d*, suture for alisphenoid. Original type figures. (After Lambe.)

In describing the splenial Mr. Gilmore on p. 96 of his memoir says 'On the internal surface, just posterior to the symphysis is an elongated oval foramen that probably represents the internal mandibular foramen of the crocodile, though in this case it appears to be wholly enclosed by the splenial while in the crocodile the splenial only forms the anterior border.' In the mandible from Red Deer river the internal mandibular foramen is shown in its usual posterior position partly enclosed by the angular. A number of small foramina occur anteriorly in the upper surface of the dentary in an irregular line close to the alveoli on their inner side. The inner portion of the dentary behind the eighth tooth is missing but it appears to have enclosed the alveoli as far back as the thirteenth, judging from a portion of a dentary bone (cat. No. 780) that includes the sockets for the fifth tooth to the twelfth. Posterior to the thirteenth tooth the splenial probably formed the inner boundary of the alveoli. In the ramus under consideration the splenial has been broken away above from the eighth tooth backward, but is partly preserved below as far back as the sixteenth.

The other elements of the ramus preserved are the angular and the surangular. These two bones overlap each other to some extent, the thin vertical surangular passing down within the angular, the overlap immediately behind the external mandibular foramen amounting to 13 mm. Both the surangular and angular are imperfect anteriorly, but in the former the upper posterior margin of the large exterior foramen is preserved (*a*, figs. 1 and 1*a*) whilst in the latter the lower posterior half of the small interior foramen is clearly shown (*b*, figs. 1 and 1*a*). The surface of contact for the articular is seen on the inner posterior surface of the surangular.

Exteriorly the ramus exhibits very rugose sculpture in its hinder half. Here the surface of the surangular from near its upper border to its junction with the angular is broken into an irregular network of ridges enclosing deep depressions and pits elongated horizontally. The surface of the angular is also rough but in it the sculpture consists principally of ridges, following the curve of the lower margin of the jaw, and separated by deep and rather irregular grooves. The dentary on the whole of its outer and lower surface exhibits numerous scattered vascular openings leading obliquely forward into the interior of the bone. Its lower surface anteriorly is roughened by numerous longitudinal grooves inclined toward the symphysis.

The specimen (cat. No. 808) shown in plate I, fig. 2, is the anterior end of a ramus larger than the type. The alveoli of the first five teeth are preserved with the base of the large fourth tooth still in its socket and enclosing a successional tooth within. This specimen gives the form of the whole of the anterior end of the ramus and supplies that part of the symphysis in which the type specimen is deficient. It shows the front termination of the dentary groove and the surface to which the splenial was applied.

Measurements of left ramus of mandible.

	MM.
Estimated length of ramus.....	335
Breadth of ramus through centre of alveolus for fourth tooth.....	31
Height of symphysis in line with same alveolus....	18
Estimated length of symphysis.....	57
Length of symphysis preserved.....	33
Length of splenial contribution to symphysis....	11.5
Length of postsymphysial foramen.....	7.5

Measurements of left ramus of mandible. (*Continued*)

Height of same.....	3.2
Height of splenial behind above foramen.....	16
Breadth of dentary at alveolus for eighth tooth...	18
Height of same in line with same alveolus.....	17.5
Height of ramus at posterior end of external mandibular foramen.....	53
Thickness of angular a little above lower border where last measurement was taken.....	16
Thickness of surangular at upper border ditto....	8.5
Length occupied by alveoli from fourth to eigh- teenth tooth.....	128

POSTERIOR PORTION OF THE CRANIUM.

The specimen already mentioned as the posterior portion of a cranium (cat. No. 1551) includes that part of the skull behind an imaginary transverse plane passing vertically downward from the frontal suture of the coalesced parietals. The squamosals, post frontals and quadratojugals are missing but the quadrates are preserved almost in their entirety. The sutures are clearly seen and the foramina in the occiput are well preserved. The interior of the brain case is exposed to view from the front showing the sutures of the parietal, the alisphenoids and the pro-otics. The walls of the brain case, however have suffered considerable damage and are broken away in the neighborhood of the internal auditory meatus on both sides. A separate frontal bone and separate jugals admit of some idea being formed of the relative size of the orbits.

Viewing the specimen from above (plate III, fig. 9), the bone formed of the coalesced parietals occupies the central position with the inner halves of the supratemporal vacuities bounding it laterally in front. Posteriorly on either side of the parietal bone is the suture for the squamosal both of which bones are unfortunately missing. The squamosal with the postfrontal (also lost on both sides) apparently completed the margin of the supratemporal vacuity without the intervention of the frontal. This last bone, judging from a specimen found separately, and to be described later, seems to have taken no part in the formation of the opening (or at most reached the border only for a very short distance), the postfrontal and the parietal nearly, if not actually, meeting behind it. In sutural contact with the parietals below are the widely extending quadrates. On the lateral anterior edge of each of these bones is seen the suture for the quadratojugal, *b*, plate III, fig. 9, and on the upper surface the suture for the squamosal, *c*, plate II, fig. 3, and Plate III, fig. 9. Overlapping the quadrate and joined to it in a broad sutural surface behind is the alar extension of the exoccipital, imperfect at its lateral extremity in each case. On the upper surface of the quadrate between this suture and the inner edge of its condyle is the small foramen *d*, figs. 3 and 9, which connects by a canal with the tympanic cavity and also is, in life, in communication with the interior of the articular bone of the mandible.

In a posterior view of the specimen, plate II, fig. 3, the position and relative size of the several elements composing the occiput are clearly shown as the sutures are well preserved and can be traced without difficulty. Comparing the occiput with that of *Diplocynodon hantoniensis* (Wood) as described and figured by Owen in his

Monograph on the Fossil Reptilia of the London Clay,¹ &c., under the name *Crocodylus hastingsiæ* (Eocene of Hampshire), p. 39, plate VI, fig. 2, it is seen to be narrower in proportion to its height. The parietal bone appears to a slight extent in the occipital aspect of the specimen. Beneath it is seen the supraoccipital, of the same breadth above as the parietal is behind, reaching downward to within a short distance of the upper edge of the *foramen magnum*. Meeting in the median line above the foramen magnum and forming the upper and lateral boundaries of that opening are the large exoccipitals which meet the basioccipital below and are produced laterally over the jugals in an extensive sutural union. The exoccipitals are prolonged downward, at their inner ends, exterior to the basioccipital. This latter bone forms the lower boundary of the foramen magnum and is deeper than broad, its upper half lying between the downward extensions of the exoccipitals. In the occipital view the basisphenoid is almost completely hidden by the basioccipital. Between these two bones at their lower extremities is the opening of the median Eustachian canal, M. E. C., plate II, fig. 3. Four foramina pierce the exoccipital; of these, three are close together in line with the mid-height of the foramen magnum. They are, in order receiving from this opening, the foramen for the *hypoglossal nerve*, XII, fig. 3, the foramen for the *vagus* or *pneumogastric nerve*, X, fig. 3, and one, the largest, for the *facial nerve*, VII, fig. 3. Near the lower extremity of the exoccipital is the foramen for the entry of the *internal carotid artery*, C. A., fig. 3.

The position of the *external auditory meatus*, leading into the *tympanic cavity* is seen at *e. a. m.*, plate III, fig. 9. The specimen here has suffered considerable damage so that the intricate structure of this part of the cranium cannot be satisfactorily made out.

Leading back from the tympanic cavity is a canal through which passed the cartilaginous rod that during the life of the animal was continuous with *Meckel's cartilage* in the mandible. The floor of this canal is seen at *e*, plate II, fig. 3 and plate III, fig. 9, in the upper surface of the quadrate. This canal thus has its exit behind between the quadrate and the lateral wing of the exoccipital as in modern alligators and crocodiles.

In side view, the occiput, leaving out of consideration the occipital condyle (which is broken off from the specimen), extends farthest back in the neighborhood of the foramen magnum; the upper half, which is concave, inclines decidedly forward up to the parietal, and the lower half to a somewhat greater extent forward in passing down to the lower extremity of the basioccipital. Viewing the specimen from this standpoint the basisphenoid appears on the surface as a narrow strip of bone between the pterygoid and the basioccipital below, and the quadrate and basioccipital above. It reaches farther down than the basioccipital and ends above, in contact with the quadrate, in line with the floor of the foramen magnum. The quadrate extends downward to meet the pterygoid, its lower extremity being at about the same level as the lower end of the downward extension of the exoccipital.

Anteriorly the quadrate bounds the pro-otic and alisphenoid behind and meets the parietal from below in a horizontal suture. The large *foramen ovale*, the opening for the passage of the *trigeminal nerve*, is preserved. It is bounded behind by the *prootic* and in front by the alisphenoid. Anteriorly the *rostrum* of the basisphenoid is broken off, leaving exposed the pair of foramina that lie immediately beneath the *pituitary fossa*. These two foramina provide for the passage of the carotid arteries.

¹Palæontographical Society, London, 1850.'

In advance of the basisphenoid are the coalesced pterygoids of which only a small portion remains in the median line clasping the anterior face of the basisphenoid. The posterior narial opening is not preserved but a small part of the roof of the narial passages remains in the pterygoid fragment immediately in front of where the opening evidently was. This roof (inclined upward and forward at an angle of 45 degrees to the horizontal) exhibits two longitudinal channels, side by side, each of which consists of a succession of oval or oblong shallowly excavated depressions placed end to end.

Within the brain case the sutures between the parietal and the alisphenoids are well shown as well as those between the latter and the pro-otics. Behind the parietal and bounding the pro-otic above in rear is part of a bone that is evidently the epiotic. The basisphenoid appears in the floor of the brain case in advance of the basioccipital. The pro-otics rise from the superior border of the former posteriorly and reach forward below the foramen for the trigeminal nerve. The roof and sides of the brain case are considerably damaged behind as are also the walls of the tympanic cavities.

Cranial measurements.

	MM
Width between outer edges of quadrates, posteriorly.....	201
Height of occiput, in median line, from upper surface of parietal to anterior edge of opening of median Eustachian canal.....	90
Height of foramen magnum.....	14
Width of same.....	17
Height of basioccipital, in median line.....	42.5
Breadth of same at mid-height.....	39
Height posteriorly of supraoccipital, in median line.....	21.5
Breadth of condyle of quadrate.....	39
Height of same at centre.....	15
Breadth of upper surface of parietal posteriorly.....	43
Length of upper surface of parietal, in median line.....	38
Thickness of parietal anteriorly, in median line.....	12.5
Breadth of exposure of basisphenoid, anteriorly in advance of pro-otics..	30
Breadth of coalesced pterygoids at junction with lower extremity of quadrate.....	40
Width of brain cavity at its mid-height, above foramen for trigeminal nerve.....	19.5
Height of same at centre, in line with same foramen.....	26
Height of exposed lateral surface of basisphenoid behind.....	44
Breadth of same exposed surface at mid-height.....	11
Length of surface preserved of roof of narial passage.....	19
Width of same behind.....	10
Distance of posterior end of same to anterior edge of opening of median Eustachian canal.....	16

SEPARATE FRONTAL BONE.

The separate frontal bone (cat. No. 1404, pl. V, figs. 14 and 14a) has a general outline, seen from above, very similar to that of the uppermost plane surface of the parietal bone. It is broad behind and narrow in front with a maximum breadth about equal to its length. Its sides are excavated for a distance of nearly three-fourths of its

length from the front by the inner border of the orbital opening which greatly reduces the anterior breadth of the bone. Laterally in front are the sutures for the prefrontals, *a*, plate V, fig. 14, between which is a small fractured surface indicating apparently where the front forward prolongation of this bone, that probably was partially overlapped on either side by the prefrontals and more anteriorly by the inner back edges of the nasals, is broken off. The suture for the parietal, *b*, figs. 14 and 14*a*, extends the full breadth of the bone posteriorly. On either side behind the orbital emargination is the suture, *c*, fig. 14, for the postfrontal. The upper surface is ornamented with large pits wider than the narrow ridges separating them. These pits occur with a decided bilateral symmetry. The whole of the under surface of the bone is free and smooth with the exception of an area on either side posteriorly for the sutural junction of the alisphenoids, *d*, fig. 14*a*. Between these sutural surfaces is the continuation of the concave roof of the brain cavity which narrows rapidly and extends forward (over the olfactory tract of the brain), as an axial groove, to the prefrontal sutures. Laterally the surface slopes evenly upward and outward to the orbital emarginations of the upper surface.

SEPARATE JUGAL.

The separate left jugal, plate IV, figs. 11 and 11*a*, is roughly rhomboidal in lateral outline. It is robust behind where it gives off superiorly the process, *pb.*, that contributes with the transpalatine to the formation of the postorbital bar. Behind the process the specimen remains thick but narrows rapidly for a short distance, beyond which in this and in five other jugals of different sizes the part that is applied to the quadratojugal is missing, the fracture in each case being a short distance behind the postorbital bar. On the inner surface of the process and extending downward and forward is the suture the *tpl.*, for the transpalatine. In advance of the suture the bone is excavated and continued forward to a point as a thin plate between the lachrymal and the maxilla which it meets in the long sutures, *l.* and *mx*, defining the anterior end of the bone. Between the posterior end of the lachrymal suture and the process is the free edge that forms part of the outer margin of the orbit. Behind the process the bone aids in the enclosure of the *lateral temporal fossa*. A number of foramina occur in the inner surface of the bone as shown in fig. 11*a*. The convex exterior surface is irregularly and very rugosely sculptured with deep pits enclosed by narrow ridges. One of the jugals is larger than the figured and most perfect specimen and four are smaller, the least being between one-third and one-half the size of the one figured. All agree in general proportions and in the style of sculpture.

ANTERIOR END OF MAXILLA.

The anterior end of a right maxilla (cat. No. 783, plate III, figs. 10 and 10*a*) has preserved in it the alveoli for three teeth behind the suture for the premaxilla which is shown in full. This suture, *pm.*, is short and runs slightly backward in its inward course. On the inner side is a straight suture, *n*, for the nasal. A prominent feature in this specimen is its rapid increase in breadth behind the premaxillary suture indicative of a short and broad snout. In advance of the first of the three alveoli (viz. those for the sixth, seventh and eighth teeth) and between it and the outer end of the suture is a shallow but decided notch, *m*, into which the fourth lower tooth evidently fitted. This notch is not so marked as the one figured by Ludwig in connexion with his description of *Crocodylus ebertyi* from the Lower Miocene (Upper Oligocene) of the

Mayense basin.¹ In many particulars there are points of resemblance between the Alberta species and *C. ebertsi* as well as *Alligator darwini*, Ludwig, also from the Upper Oligocene of the Mayense basin (Weissenau) (op. cit.) both of which species are referred by Lydekker² to the genus *Diplocynodon*. The same authority regards *D. ebertsi* as identical with *D. gracile*, Vaillant, already mentioned in describing the mandible. The upper surface of the maxillary fragment is concave and rises rapidly behind; it is rendered rough by irregular, short, longitudinal ridges. A few vascular foramina occur a short distance above the alveolar border and smaller ones behind the suture for the premaxilla. Beneath, the thin plate-like inward continuation of the bone forming part of the palate, is broken away not far from the alveoli, exposing the longitudinal excavation for the narial passage. Here also are small foramina near the inner alveolar border. The three alveoli are placed close together and are of fair size, the first (that of the sixth tooth) being the smallest. The palatal part of the bone presents a plane surface and there are no pits for the reception of the lower teeth, viz. those behind the fourth which are all of small size, at least up to the tenth. It is probable that all the lower teeth behind the fourth fitted within the upper teeth. The enlarged lower third tooth in addition to the fourth probably was received into a notch of which only half was contributed to by the maxillary bone. The obliquity of the first three alveoli of the mandible is suggestive of an interlocking of the anterior lower and upper teeth. Attention may here be drawn to the fact that the third and fourth lower teeth of *Diplocynodon ebertsi* (Ludwig) are received into a notch in the maxilla behind the premaxillo-maxillary suture. From this specimen it is impossible to tell how far the nasals extended but judging from the straightness of the nasomaxillary suture it is probable that they reached a point in advance of the maxillaries.

TEETH.

The teeth, of which there are over sixty, found separately, are in shape elongato-conical and slightly curved. The crown bears on each side a distinct, sharp-edged ridge placed a little toward its inner surface and extending from the apex to near the base. These ridges define laterally an area on the inner surface that is less convex than the outer surface and in breadth slightly exceeds one-third of the circumference of the tooth.

The Alberta teeth vary considerably in size. The larger ones are broad in proportion to their length; the smaller ones are comparatively slender. Most of them show signs of wear and in many, more particularly the slender ones, a faint longitudinal fluting is observed generally most apparent at the mid-height of the crown on the inner face. The majority of them appear to have been shed. The upper end of the pulp cavity is indicated by a small excavation in the base of the crown.

In the anterior end of the right ramus, shown in pl. I, fig. 2, the base of the fourth tooth is preserved and exceeds in diameter that of any of the teeth found separately. Within this base is a successional tooth (indicated in the figure) that agrees in shape and enamel marking with other germ-teeth in the collection. These show the lateral keels meeting at the apex and have a lustrous surface caused by minute, longitudinal wrinkles in the enamel converging to the point.

The height of the crown relative to the basal breadth in a few of the specimens is given by the following measurements in mm., the height being the first of each pair

¹Palæontographica, supplement, vol. III, pt. IV, 1887, p. 31, Pl. III, fig. 5.

²Catalogue Fossil Reptilia and Amphibia, Brit. Mus., pt. I, 1888, pp. 46 and 50.

of numbers:—21–10, 20–11, 17–20, 22–9, 17–8, 15–8, 14–7.5, 13–7, 13.5–5, 11.5–6, 11.5–4.5, 11–4, 10–5, 8–4, 7–4.5.

VERTEBRÆ.

The vertebræ from Alberta are of the procœlian type and resemble in general form those of the living Crocodilia. They were found separately and are from the cervical, dorsal, sacral and caudal regions. They include two second sacrals and a first caudal.

The largest and most complete specimen is regarded as a late dorsal, plate IV, figs. 12, 12*a*, although, as the bases only of the transverse processes remain, it is possible that it is one of the lumbar vertebræ. The zygapophyses are preserved as well as the neural spine from which the tip is broken off. The centrum is well excavated in front and is convex behind. Its inferior surface is flat and laterally it is slightly pinched beneath the mid-height. It increases in breadth beneath the suture for the neural arch which is robust and rises from the dorsal surface of the centrum. The neural canal is narrow and high. The neural spine and the zygapophyses present no unusual characters and resemble somewhat those of a living crocodile. The transverse processes are given off well up on the neural arch about on a level with the mid-height of the neural canal. The zygapophyses with the bases of the transverse processes at a slightly lower level, together form an undulating platform of considerable extent.

Measurements of dorsal vertebra, cat. No. 1508,	MM.
Length of centrum.....	33
Anterior height of same.....	22.
Breadth of anterior end of same above mid-height.....	27
Distance apart of outer edges of prezygapophyses.....	47
Width of neural canal.....	11
Height of same.....	15

With the exception of a centrum representing a dorsal vertebra about the size of the above, the other specimens from the dorsal (or lumbar) region are smaller and belonged to younger individuals; the only differences noticed would be those resulting from a difference of position in the series.

The cervical vertebræ are represented by centra of small size. The best preserved centrum (cat. No. 1908) is short and deeply excavated laterally. The anterior articular face is concave, the posterior one convex. On each side inferiorly is a facet for the articulation of the capitulum of the cervical rib. The other cervical centra are similar to the above specimen and show the facet for the rib in a like forward position. One of the specimens is larger than the others but otherwise is the same and gives no additional information.

Measurements of cervical centrum, cat. No. 1908.	MM.
Maximum length.....	19
Anterior breadth.....	19.5
Height of anterior face in median line.....	11
Breadth of posterior face.....	16
Height of posterior face in median line.....	11.5

The better preserved of the two second sacral vertebræ is shown, viewed from behind, in plate IV, fig. 13, (cat. No. 1010); some measurements taken from it are as follows:—

	MM.
Maximum length of centrum.....	27
Breadth of posterior articular face of same.....	16
Height of posterior articular face of same.....	13
Width between outer edges of postzygapophyses.....	22
Breadth from median line of centrum to distal end of sacral rib (imperfect)	32
Height of neural canal posteriorly.....	10.5
Width of same posteriorly at mid-height.....	8
Breadth of anterior articular face of centrum.....	16.5
Height of same.....	11.5

SCUTES.

The dermal armour is represented by over fifty pitted scutes none of which with certainty can be said to have belonged to the ventral surface. The majority of the scutes are nearly square or oblong with rounded angles and a smooth, flat or transversely concave under surface. Those that are flat (or somewhat convex) beneath usually have the pits of the upper surface disposed without apparent order, those in which there is a decided transverse curvature to the plate (causing the under surface to be slightly concave) generally have a low, longitudinal keel developed above, from which the pits diverge on either side to a greater or less extent, with a tendency to show a radial pattern. In some specimens the keel extends the full length of the plate, in others it is shorter or it may be reduced to a central raised area in which case the radiating arrangement of the pits becomes more pronounced. The scutes range in breadth from about 15 to over 50 mm. It is thought that those without keels may have belonged to the ventral surface.

The pits are conspicuous, deep depressions separated from each other by a reticulation of smooth, narrow ridges. They vary in size considerably, their outlines being roughly circular, quadrilateral or polygonal with rounded angles, or oval with the major axis of the elongated ones in a direction as a rule at right angles to the margin of the scute. The supposed ventral scutes are ornamented with pits that show little variation in size and are nearly circular in outline.

A dorsal scute is shown in plate V, fig. 15. It is broader than long, with a short longitudinal keel or central raised area from which the pits radiate. It is thickest (4.5 mm) at the centre and thins gradually in all directions outward; the front and hinder borders coming to a sharp edge. The sides retain a thickness of nearly 2 mm., and are rough having probably been in contact with a scute on each side. The surface is smooth for a short distance back from the front edge forming a marginal tract that was overlapped by the scute immediately in front. The under surface is quite smooth and in a transverse direction slightly concave.

Figures 16, 17 and 19 give representations of the scutes in which the keel extends almost their full length. These scutes have not a well defined smooth area indicative of having been overlapped. The edges in front and behind are thin but the lateral edges are rough particularly in the two smaller specimens (figs. 17 and 19) which exhibit sutural surfaces of some thickness (about 4.5 in fig. 17). The under surface, in the three, is transversely concave.

A small almost circular scute (fig. 20) has a very decidedly concave under surface. Its front and back edges are sharp, the lateral ones comparatively thick.

The long very deeply pitted scute represented in fig. 18, has a slightly convex under surface. Its edges are slightly irregular, not very thin and nowhere exhibit what would constitute a sutural surface.

A supposed ventral scute, fig. 23, has no keel; it is almost square and slightly convex above and below. It thins toward the edges but much less toward one side (the left in the figure) where the edge is, at its mid-length, about 2.5 mm. thick and evidently forms a definite sutural surface. This scute may be one of two pieces composing a compound ventral plate similar to those of species of *Diplocynodon*.

Two scutes, plate V, figs. 21 and 22, are conspicuous on account of their size. One fig. 21, is very decidedly bent so as to be transversely very concave beneath. A short longitudinal keel is developed and laterally the edges remain thick and rugose. The other is flat below, is without a keel, and no evidence of sutural contact with other scutes is recognizable; it is possible that this scute is from the upper surface of the neck and formed part of a neck-shield.

The maximum thickness of each of the scutes figured in plate V is given in the following measurements:—fig. 15, (cat. No. 1146), 4.5 mm.; fig. 16, (cat. No. 1705) 7.5 mm.; fig. 17, (cat. No. 1527), 5 mm.; fig. 18, (cat. No. 975), 4.5 mm.; fig. 19, (cat. No. 1837), 3 mm.; fig. 20 (cat. No. 1614), 3 mm.; fig. 21 (cat. No. 377), 9 mm.; fig. 22, (cat. No. 960), 9.5 mm.; fig. 23, (cat. No. 869), 4 mm.”

The species may be considered valid.

***Leidyosuchus sternbergii* Gilmore**

ORIGINAL TYPE REFERENCE.—GILMORE, C. W., 1910, ‘*Leidyosuchus sternbergii*, a New Species of Crocodile from the Ceratops Beds of Wyoming,’ Proc. U. S. Nat. Mus., XXXVIII, pp. 408–502, 2 figs., Pls. XXIII–XXIX (Pub. No. 1762).

SUBSEQUENT REFERENCE.—None exists at the present time to the best of the writer’s knowledge.

ORIGINAL TYPE FIGURES.—GILMORE, C. W., 1910, ‘*Leidyosuchus sternbergii*, a New Species of Crocodile from the Ceratops Beds of Wyoming,’ Proc. U. S. Nat. Mus., XXXVIII, pp. 405–502, figs. 1, 2, Pls. XXIII–XXIX.

TYPE.—Greater portion of the skull, left mandibular ramus, anterior part of right ramus, eight vertebræ, both humeri, right fibula, second left metatarsal and fragmentary parts of skeleton. U. S. Nat. Mus. No. 6533.

TYPE LOCALITY AND LEVEL.—North side of Cheyenne River, Converse County, Wyoming. Ceratops Beds.

ORIGINAL TYPE DESCRIPTION.—“Viewed from above the form of the skull resembles that of the living crocodile, although compared with *Crocodylus americanus* it is proportionally broader posteriorly, approaching nearer in its general outline the skull of *C. porosus*. Evidently the specimen is that of an adult as shown by the complete coalescence of many of the sutures. A section across the whole width of the median preorbital region and extending back on the right posterior half of this aspect has been lost through erosion. In Pl. 23 is shown a superior view of the skull, reproduced here from a photograph taken after the missing parts were restored. The lighter color of the restored parts distinguishes them at once from the original fossil.

The coalesced parietals occupy the posterior median position, their anterior lateral borders forming the inner boundaries of the supratemporal fossæ. The least

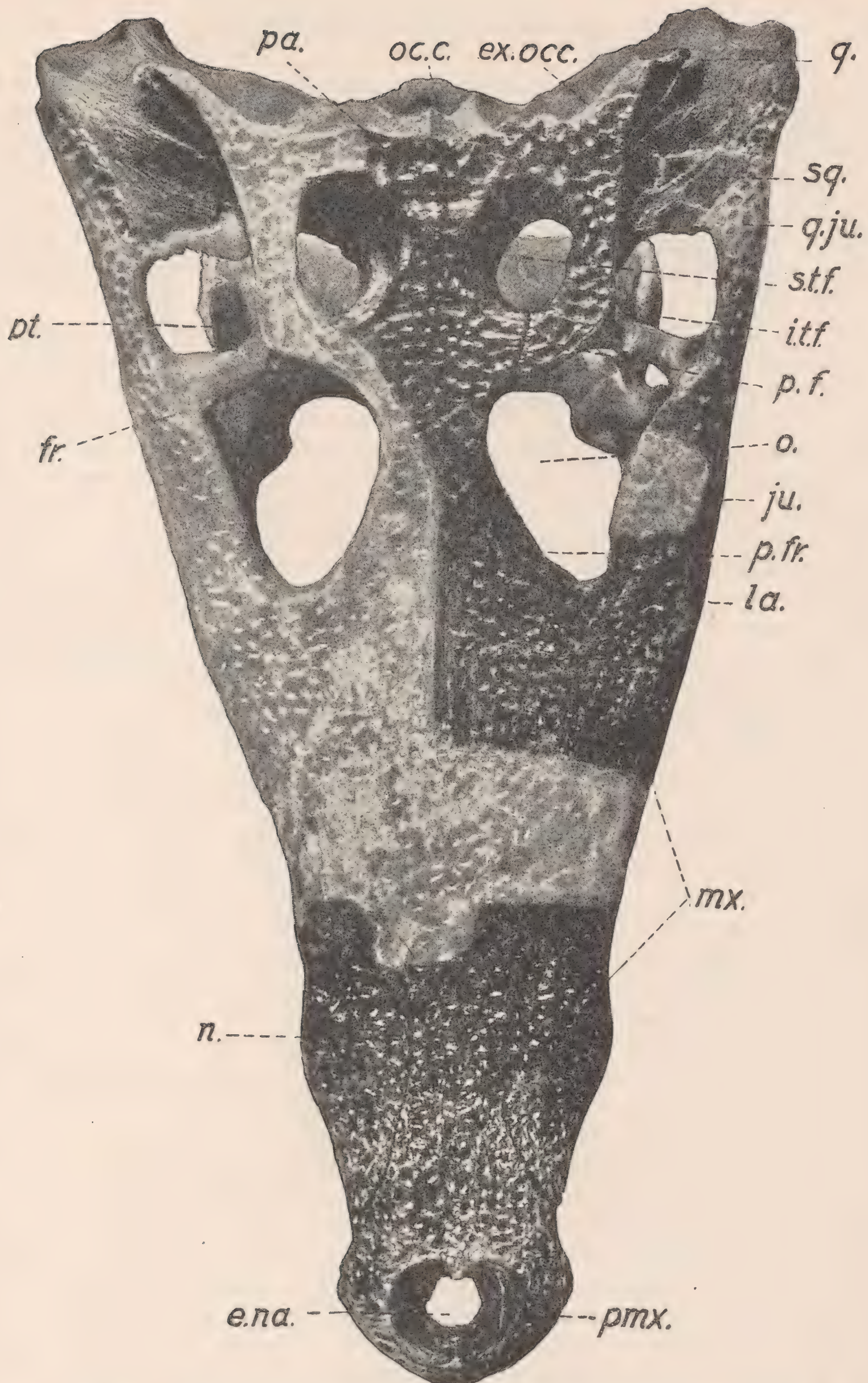


Fig. 48. *Leidyosuchus sternbergii* Gilmore. Type specimen, skull (U. S. Nat. Mus. No. 6533).

One-half natural size. Superior view; *e. na.*, external nares; *ex. occ.*, exoccipital; *fr.*, frontal; *i. t. f.*, infratemporal fenestra; *ju.*, jugal; *la.*, lachrymal; *mx.*, maxillary; *n.*, nasal; *o.*, orbit; *oc. c.*, occipital condyle; *pa.*, parietal; *p. f.*, postorbital (postfrontal in Gilmore's caption); *p. fr.*, prefrontal; *pmx.*, premaxillary; *pt.*, pterygoid; *q.*, quadrate; *q. ju.*, quadratojugal; *s. t. f.*, supratemporal fenestra; *sq.*, squamosal. Original type figure. (After Gilmore.)

width of the parietals between these vacuities is 17 mm. The posterior half of the dorsal surfaces of the parietals is covered with large, deep, irregularly shaped pits, while on that portion between the fossæ there is a single median longitudinal ridge with comparatively smooth tracts on either side which extend laterally to a smooth, raised ridge of bone around the inner and posterior boundaries of the supratemporal vacuities. The suture between the parietal and squamosal of the left side can not be distinguished, but as shown in *L. canadensis* their union is probably at the middle of the posterior boundary of the supratemporal fossa.

The union of the parietals with the frontal is only dimly discernible, but on the inner anterior surface of the left supratemporal fossa the suture is quite distinct and shows clearly that the frontals contribute to the boundary of the fossa on the superior surface between the parietal and postfrontal, as in *Diplocynodon* Pomel. Two detached but broken parts of the frontal bone, which were found near this specimen and which supplement each other, may, from their size and sculpturing, be considered as belonging to the present species, and shows that this bone was broad behind and narrow in front. In the type skull the side of the frontal is excavated for a distance of 18 mm. by the inner border of the orbit. The posterior upper surface is ornamented with well-defined pits, smaller than those found on the same surface of the parietals. These pits vary in size and shape from subround to elongate-oval, being arranged in transverse rows and separated by ridges narrower than themselves; none are confluent. The larger pits have their greatest diameter transversely. The median anterior portion is without decided ornamentation, as best shown in a detached frontal (Cat. No. 6542, U. S. N. M.). The whole of the under surface is smooth except an area on either side posteriorly for the sutural union with the alisphenoids, where it forms a considerable part of the roof of the cranial cavity. Between the alisphenoids is a median longitudinal depression, which carries the sense organs to the olfactory lobes of the brain. This groove traverses the whole length of the bone, widening anteriorly to the fronto-prefrontal suture. Posteriorly, this suture can only be made out on the inner orbital surface where it occupies approximately the same position as in *C. americanus*, and on the orbital side runs obliquely downward and forward.

The squamosal meets the quadrate and exoccipital below and forms part of the roof of the external auditory meatus. It is pitted above, and, with the prefrontal, [evidently referring to the postorbital] forms the outer boundary of the supratemporal fossa. The postfrontal unites as usual with the jugal by a strong postorbital bar. The shape or extent of the nasals, prefrontals, or lachrymals can not be determined in this specimen, as all of the sutures are obscure. These bones are roughly sculptured. That portion of the preorbital region which is preserved in this specimen is depressed medially and at the sides is bent sharply downward and inward to the alveolar border; more anteriorly the direction of the side is only downward. As a whole, the snout is bent somewhat upward, so that in profile the anterior portion is slightly concave above. (See Pl. 25.) The cranium above and extending down the sides on the jugal, maxillary, and premaxillary bones is beautifully sculptured with pits of irregular size and shape, inclosed by reticular ridges of varying widths. The sculpturing is most rugose on the posterior elements, particularly on the jugal and posterior half of the maxillary; medially on the nasals, are long, broken, longitudinal grooves, while on the muzzle the pitting as a rule is finer and more shallow, and lacks the definition of the posterior surfaces.

Over the alveoli for the ninth and tenth teeth, the lateral borders of the maxillæ are swollen outwardly, but anteriorly the muzzle gradually contracts to the elongated

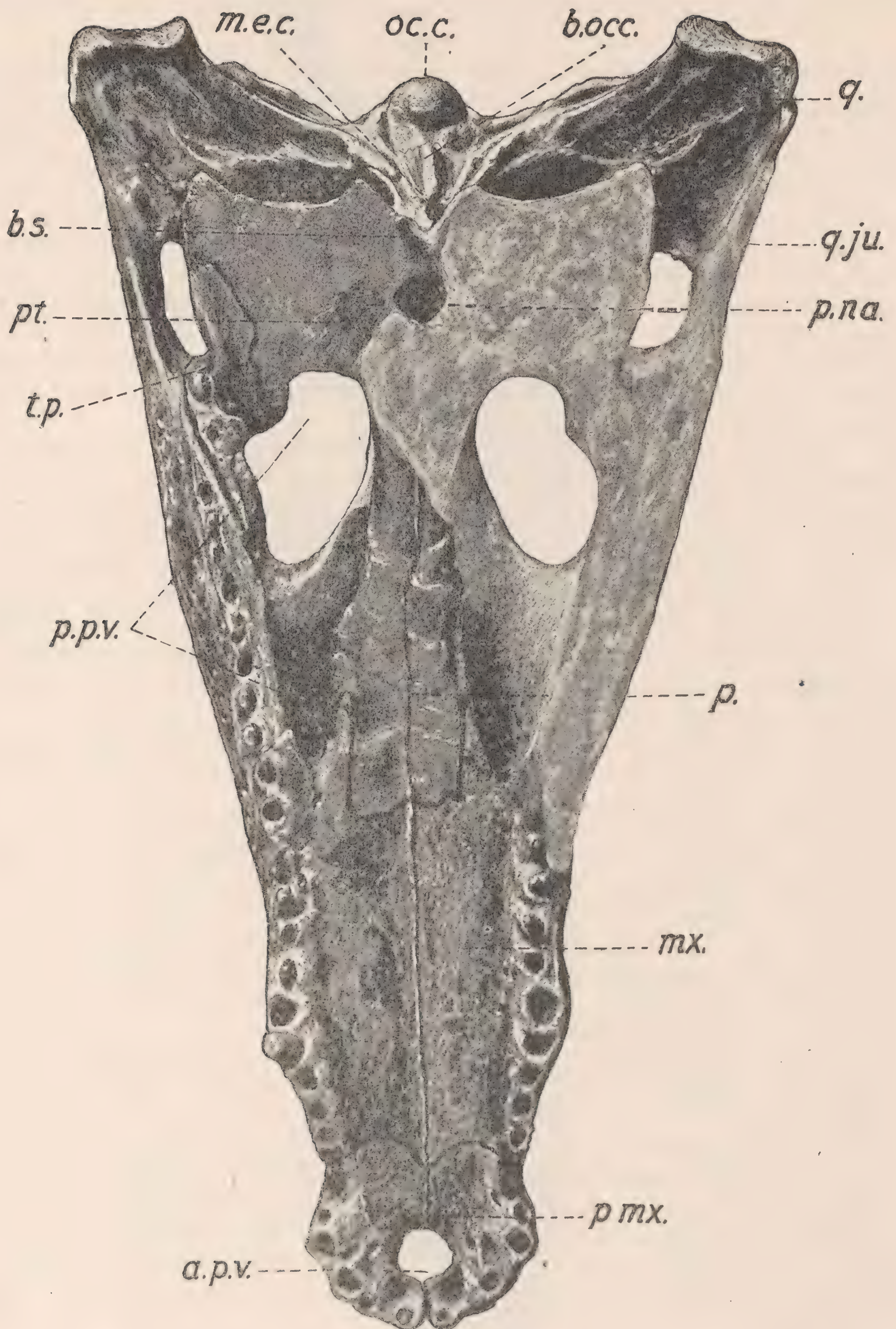


Fig. 49. *Leidyosuchus sternbergii* Gilmore. Type specimen, skull (U. S. Nat. Mus. No. 6533).

Inferior view; *a.p.v.*, premaxillary foramen; *b.occ.*, basioccipital; *b.s.*, basisphenoid; *m.e.c.*, median Eustachian canal; *mx.*, maxillary; *oc.c.*, occipital condyle; *p.*, palatine; *p.mx.*, premaxillary; *p.na.*, posterior nares; *p.p.v.*, palatine fenestra; *pt.*, pterygoid; *q.*, quadrate; *q.ju.*, quadratojugal; *t.p.*, ectopterygoid. Original type figure. (After Gilmore.)

notch which receives the lower canines, this being the narrowest part of the skull, measuring 50 mm. in transverse diameter. In advance of the notch the premaxillæ swell out into a moderately broad but evenly rounded nose. The widest part, over the fourth premaxillary teeth, measures 58 mm.

The premaxillæ inclose the heart-shaped external nares, but it can not be determined from this specimen whether or not the nasals extended into this opening. In *Diplocynodon hautoniensis* (Wood), which Owen figures in his monograph . . . under the name *Crocodylus hastingsiæ*, the nasals do not reach the narial opening, and taking into account the many other resemblances it may be that the same condition prevails in the nasals of *Leidyosuchus*. Lambe, from incomplete evidence, was inclined to believe the nasals reached a point in advance of the maxillaries in *L. canadensis*, and if his observation be correct, they at least approach the nares more closely than in *Diplocynodon*.

The posterior extent of the facial processes of the premaxillæ can not be determined, although the maxillo-premaxillary and maxillo-nasal sutures can be traced (see Pl. 23) back as far as the missing facial section previously mentioned. Latero-inferiorly the posterior boundary of the premaxillary is at the back of the notch behind the fifth tooth, where the maxillo-premaxillary suture passes on to the palate.

The supratemporal fossæ are of good size and subelliptical in shape, measuring 33 mm. longitudinally and 23 mm. transversely. The orbit communicates with the infratemporal fossa. The latter are slightly smaller than the supratemporal fossæ and angularly rounded. The left fossa, the borders of which are nearly intact, measures about 25 mm. both transversely and antero-posteriorly.

The orbits are large and look upward and forward, with their inner borders everted as in the alligator. The greatest longitudinal diameter of the left orbit is 55 mm. and the transverse diameter 38 mm.

The inferior or palatal surface is more complete than the dorsal, lacking only the posterior ends of the palatines, the right pterygoid, transpalatine, and posterior half of maxillary of same side. The anterior palatal region is decidedly concave transversely, and between those elements which have not suffered mutilation all of the sutures are plainly distinguishable. The palatine processes of the premaxillæ reach the level of the alveolus for the first maxillary tooth, the posterior ends being rounded. In this view the premaxillæ inclose a small rounded anterior palatine vacuity which measures 12 mm. longitudinally and 13 mm. transversely.

The anterior processes of the maxillæ extend forward on the median line to the level of the middle of the notch which separates the maxillary and premaxillary dental series.

The palatines meet the maxillæ at the center by a nearly straight transverse suture opposite the tenth maxillary tooth. The median posterior processes of the maxillæ extend back on the sides of the palatines to a point opposite the thirteenth maxillary tooth. The palatines are narrow and at the middle of the posterior palatine vacuity measure only 23 mm. in transverse diameter. Their sutural union with the pterygoids, owing to the damaged condition of this part of the palate, can not be determined.

The posterior palatine vacuities are comparatively large, measuring 101 mm. longitudinally and 34 mm. transversely. The anterior border of these vacuities is opposite the twelfth maxillary tooth, as in *Diplocynodon*.

The pterygoid of the left side is practically entire and has suffered no distortion. It extends downward and backward from the general level of the palate at an angle



Fig. 50. *Leidyosuchus sternbergii* Gilmore. Type specimen, skull and jaws (U. S. Nat. Mus. No. 6533). One-half natural size. Lateral view, left side; *ang.*, angular; *d.*, dentary; *e.m.f.*, external mandibular foramen; *ju.*, jugal; *mx.*, maxillary; *pmx.*, premaxillary; *q.*, quadrate; *q.ju.*, quadrato-jugal; *s.ang.*, surangular; *sq.*, squamosal. Original type figure. (After Gilmore.)

of 45°. The postpalatal vacuities encroach but little on the pterygoids. The preservation of the back border of the posterior aperture of the nasal passages is sufficient to establish its position as being wholly surrounded by the pterygoids. There is a bridge of bone 12 mm. wide separating this opening from the posterior median border of the pterygoids which leads down to the median Eustachian foramen. (See Pl. 24.) In all modern crocodiles these two openings are separated by only a thin septum of bone. In this respect *L. sternbergii* from the Cretaceous is intermediate between those early Triassic and Jurassic forms having the posterior narial opening well forward on the palate, and the Tertiary crocodiles where it has receded posteriorly to a position nearly, if not quite, as far as in modern crocodilians. The posterior border of the conjoined pterygoids is notched, the notch being the interval between two thin diverging processes from the back part of the pterygoids. The form of the posterior nares can not be determined from this individual.

The transpalatines connect the pterygoids with the maxilla, as shown in Pl. 24.

In the posterior view of the skull (Pl. 26) hardly any of the sutures can now be distinguished, and a comparison of this aspect with the excellent figures given by Lambe of *Leidyosuchus canadensis*, only serves to give one an approximate idea of the relations of the several elements comprising the occiput. In the proportion of its breadth to its depth, *L. sternbergii* differs from *L. canadensis* in the considerably less vertical extent of the coalesced elements overlying the foramen magnum, in the shortness vertically of the descending part of the basioccipital, and in the comparative lightness, both horizontally and vertically, of the condyle of the quadrate. In the latter respect it approaches *Diplocynodon haultoniensis* of the London Clay.

The basioccipital is deeper than broad, and viewed from behind almost hides the basisphenoid which lies in front of it. Between these two bones at their lower extremities is the opening for the median eustachian canal. (See *m. e. c.*, Pl. 26.) Below the occipital condyle on the median posterior surface of the basioccipital a prominent sharp vertical keel is developed which is even more pronounced than that found in the living alligators. Another alligator-like character is seen in the entire exclusion from this view of the posterior nostril, due to its position below the opening of the eustachian canal and in advance of the posterior border of the pterygoids, from which it is partitioned off by a strong bridge of bone 12 mm. wide.

The exoccipital is pierced by four foramina. Of these, three are close together a little above the floor of the foramen magnum Pl. 26. Beginning with the most posterior, they are (XII) foramen for the exit of the hypoglossal nerve (X) foramen for pneumogastric, and (VII) the largest of the three, which gives passage to the facial nerve and certain blood vessels. Below these, near the lower extremity of the exoccipital, is the large foramen through which the internal carotid artery enters the skull.

The external auditory meatus leading into the tympanic cavity occupies the usual position deep in under the squamosals, and compared with the same opening in *Crocodylus americanus* no essential differences are apparent. Leading back from the tympanic cavity is a canal in the quadrate through which the cartilaginous rod passes, and during life is continuous with Meckel's cartilage within the articular bone of the mandible.

Viewed from the side, the occiput above the level of the floor of the foramen magnum is inclined decidedly forward up to the parietal, and the part below this level inclined forward to a somewhat greater extent in passing down to the lower extremity of the basisphenoid, which continues below the basioccipital to meet the conjoined pterygoids.

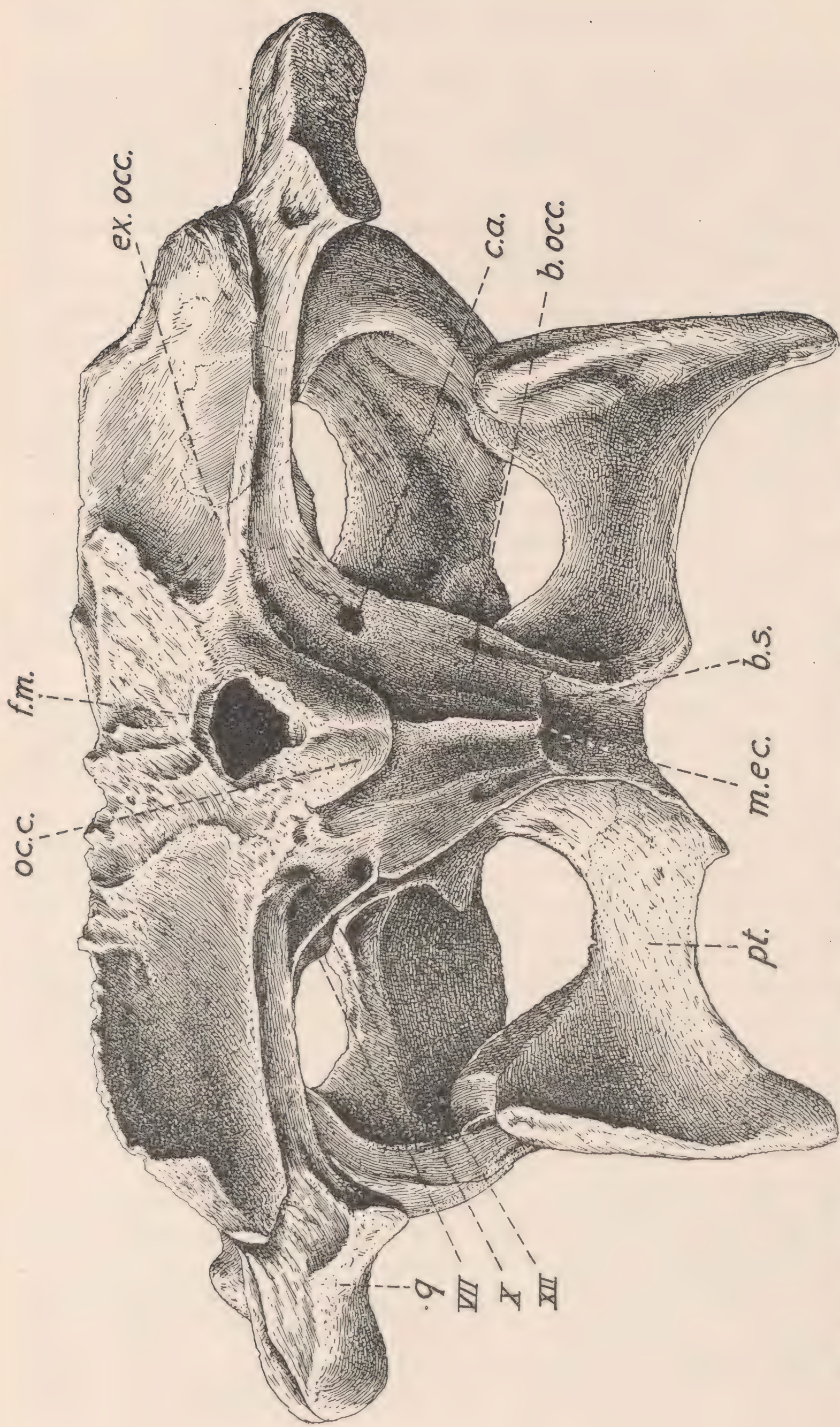


Fig. 51. *Leidyosuchus sternbergii* Gilmore. Type specimen, skull (U. S. Nat. Mus. No. 6533).

Natural size. Posterior view; *b.occ.*, basioccipital; *b.s.*, basisphenoid; *c.a.*, foramen for carotid artery; *ex. occ.*, exoccipital; *f.m.*, foramen magnum; *m.ec.*, median Eustachian canal; *oc.c.*, occipital canal; *pt.*, pterygoid; *q.*, quadrate; VII, X, XII, foramina for cranial nerves. Original type specimen. (After Gilmore.)

On account of the damaged condition of the brain case, the elements comprising it cannot be differentiated, although all the important foramina can be located. Taken in order from back to front they are: *Foramen ovali* for the trigeminal nerve; the pair of foramina lying beneath the pituitary fossa which furnish passage for the carotid arteries; and the large anterior foramen for the exit of the olfactory nerves. In all essentials the relationships of the several foramina are very similar to those found in the skull of extant crocodilians.

The teeth.—The dental formula of *Leidyosuchus sternbergii* is $\frac{2}{2}\frac{4}{1}-\frac{2}{2}\frac{4}{1}=90$. In the type-specimen we are fortunate in having fourteen teeth in the upper and three in the lower mandible in a good state of preservation, in addition to the crowns of three others found detached.

The teeth *in situ* are distributed as follows: First of the left premaxillary; fourth, sixth, seventh (germ tooth), eighth, twelfth, thirteenth, fifteenth (germ tooth), seventeenth, and eighteenth of the left maxillary; fourth (germ tooth), seventh, eighth, and ninth of the right maxillary. In the left ramus of the lower mandible are the fourth and seventeenth, with the base of the twelfth and in the portion of the right ramus is the base of the third and a young tooth in the eighth alveolus. Taken in the order mentioned above, the crowns of the teeth give the following measurements in millimeters, the first of each pair of numbers being the height; the second, the basal or antero-posterior extent: First, 4.5–3.5; fourth, 9 (tip broken off)–7.5; sixth, 6–5; eighth, 4.8–4; twelfth, 6–6; thirteenth, 5–5.7; seventeenth, 3.2–4.7; eighteenth, 2.5–4.5. Right side, seventh, 5–4.1; eighth, 5.1–4.5; ninth, 5–5.6.

Most of the teeth, excepting those enlarged, are much the same shape, with short, compressed, subacute or obtuse crowns. The crown bears on each side a distinct, sharp-edged ridge placed a little toward its inner face, and unworn crowns extending from the apex to near the base. These ridges or carina define laterally, on the shorter teeth of the series, an area on the inner surface that is less convex and slightly less in breadth than the outer surface. In most of the enlarged teeth these ridges are placed nearer together and define an area on the inner side, the breadth of which slightly exceeds one-third the circumference of the tooth. The crowns of all the smaller teeth are separated from the fang by a slight constriction or neck.

The larger teeth in cross section are more rounded and proportionately narrower transversely than the smaller, but somewhat more curved. A scrutiny of the measurements given above shows that the crowns of the posterior teeth are greater in width than in height, while in advance of the twelfth maxillary tooth the height is greater.

The anterior pair of premaxillary teeth are close together, being separated on the median line by a narrow slit, which emerges dorsally into an enlarged rounded foramen. The one preserved tooth of this pair is small and comparatively slender. The first pair is separated from the alveoli of the second pair by deep pits for the reception of the anterior mandibular teeth, which do not perforate the upper surface as in some extinct and all modern crocodiles. The second pair are small and in close contact with the alveoli for the third pair, which are much enlarged. The fourth pair appear to be a trifle larger than the third, from which they are separated on the inner side by a pit. The fifth and last pair in the premaxillaries are very small and in close contact with the fourth.

Between the fifth pair of the premaxillaries and the first of the maxillaries are elongated notches (anterio-posteriorly they measure 15 mm.) which receive the two enlarged teeth of the mandibular series.

The first three maxillary alveoli are rather small, though they increase in size from front to back. The fourth and fifth are much enlarged, and, judging from the size of the alveolus, the fourth is the most robust tooth of the upper dental series. The sixth, seventh, eighth and ninth are much reduced in size, but the tenth and eleventh alveoli appear to have carried larger teeth. From this point, however, to the end of the series, the teeth gradually diminish in size toward the back. In the lower mandibular series all of the alveoli and three of the teeth are preserved. The front teeth of the symphyisial region, that is, the first to the fourth, were directed obliquely outward. This peculiarity is somewhat manifest as far back as the eleventh of the series, back of which an upright position is maintained. The dental series of the anterior half passes in a curve from the outer to the inner side of the dentary. The fourth tooth was probably the largest of the lower series, although, judging from the alveoli, the third must have been approximately the same size. The fifth to the tenth were small. The eleventh, twelfth, and thirteenth were slightly and about equally enlarged, and those posterior to the thirteenth gradually decrease in size.

Comparative measurements of skulls.

	Holotype of <i>Leidyosuchus</i> <i>sternbergii</i>	Paratype of <i>Leidyosuchus</i> <i>canadensis</i>
	mm.	mm.
Width between outer edges of quadrates, posteriorly...	183	201
Height of occiput, in median line, from upper surface of parietal to anterior edge of opening of median eustachian canal.....	61	90
Height of foramen magnum.....	13	14
Width of foramen magnum.....	16	17
Height of basioccipital, in median line.....	37.5	42.5
Breadth of basioccipital at midheight.....	37	39
Breadth of condyle of quadrate.....	30	39
Height of condyle of quadrate at center.....	11	15
Breadth of the upper surface of parietal, posteriorly....	a40	43
Length of upper surface of parietal, in median line.....	a40	38
Distance of posterior end of preserved surface of narial passage to anterior edge of opening of median eustachian canal.....	12	16

Mandible.—The parts preserved of the lower jaw consist of the left ramus almost entire, lacking only the coronoid and portions of the articular, and the anterior portion of the right ramus as far back as the alveolus for the eleventh tooth.

The mandibular symphysis is short and composed of the splenial and dentary. In *Leidyosuchus canadensis* the splenial participation in the symphysis is about one-fifth of its total length, while in *L. sternbergii* it is somewhat less. In this particular, among American brevirostrate crocodiles, *Leidyosuchus* is approached by *Crocodylus*

“a. Estimated.”

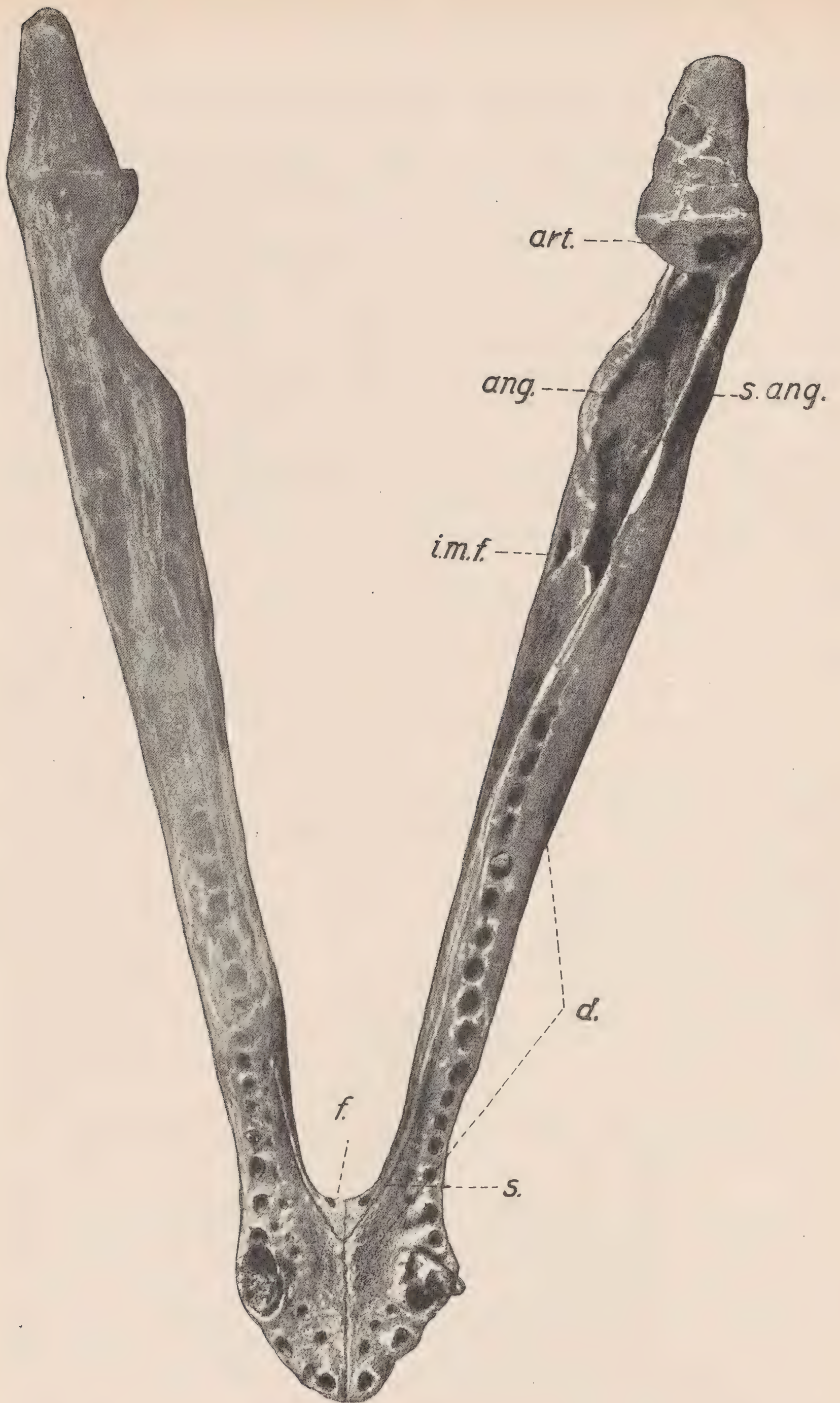


Fig. 52. *Leidyosuchus sternbergii* Gilmore. Type specimen, lower jaws (U. S. Nat. Mus. No. 6533).

One-half natural size. Superior view; *ang.*, angular; *art.*, articular; *d.*, dentary; *f.*, postsymphysial foramen; *i.m.f.*, intermandibular foramen; *s.*, splenial; *s.ang.*, surangular. Original type figure. (After Gilmore.)

polyodon of the Wasatch and *Bottosaurus* from the Cretaceous of New Jersey, in the latter the splenial reaches the symphysis without contributing to it.

On the dorsal border of the left ramus, alveoli for twenty-one teeth can be clearly distinguished.

By referring to the table of measurements it will be observed that the dimensions of the ramus of the specimen under consideration are almost identical with those of the holotype of *L. canadensis*.

Viewed from the side the alveolar border is undulating, while the lower side from a point just posterior to the external mandibular foramen presents a nearly straight border to the upturn of its extremity near the symphysial end. The external mandibular foramen is relatively large and in outline has the form of an elongated ellipse.

(See *e. m. f.*, Pl. 25.)

The internal mandibular foramen is relatively small, and in relation to the large external foramen is located more posteriorly than in living crocodilians. The position of this foramen is well shown in Pl. 27 (*i. m. f.*).

In the region of the eighth tooth the dentary is constricted, but anteriorly it widens both inward and outward, reaching its maximum breadth in line with the fourth tooth, with a transverse diameter of 32 mm. Posterior to the constriction the alveolar border ascends rapidly to the position of the twelfth tooth. From this point posteriorly the upper border rises gradually with a gentle concave curve, thus adding considerably to the depth of the jaw. The maximum depth of the ramus is just posterior to the external mandibular foramen, where it reaches 53 mm.

The dentary articulates in the usual manner with the surangular above and the angular below. The upper posterior prolongation of the dentary, however, does not extend so far back over the external foramen as in living crocodiles. The anterior extension of the angular is received between the dentary and the splenial, terminating under the alveolus for the nineteenth tooth. The external surfaces of both the angular and surangular, especially the former, are roughly sculptured (well shown in Pl. 25). The irregular pitting of the upper half of the external surface of the angular is succeeded below by long, somewhat irregular grooves and ridges which conform to the curves of the lower margin of the jaw. The dentary along the whole of its outer and under surface is pitted by numerous vascular openings leading obliquely forward into the interior of the bone. These openings become more numerous anteriorly, and on the lower part the surface is roughened by numerous longitudinal grooves.

The splenial covers the whole inside of the ramus back to the internal mandibular foramen. Just behind the symphysial union, the splenial is pierced by a small, longitudinally elongated foramen which leads into the meckelian groove. Lambe has shown that beneath this opening there is a small foramen in the dentary leading into the dental canal. Unlike the type of *L. canadensis*, the bony divisions of the alveoli form distinct sockets for the teeth and furnish additional evidence of the mature age of this individual.

The coronoid is missing.

The articular is somewhat damaged but the parts remaining show no unusual characters.

Comparative measurements of rami.

	Holotype of <i>Leidyosuchus</i> <i>sternbergii</i>	Holotype of <i>Leidyosuchus</i> <i>canadensis</i>
	mm.	mm.
Length of ramus.....	380	a335
Breadth of ramus through center of alveolus of fourth tooth.....	31	31
Height of symphysis in line with alveolus of fourth tooth	19	18
Length of symphysis.....	56	a57
Length of splenial contribution to symphysis.....	7.5	11.5
Length of postsymphysial foramen.....	6.	7.5
Height of postsymphysial foramen.....	3.	3.2
Height of splenial behind postsymphysial foramen.....	16	16
Breadth of dentary at alveolus for eighth tooth.....	11	18
Height of dentary in line with same alveolus.....	18	17.5
Height of ramus at posterior end of external mandibular foramen.....	53	53
Thickness of angular a little above lower border where last measurement was taken.....	16	16
Thickness of surangular at upper border where last measurement was taken.....	7	8.5
Length occupied by alveoli from fourth to eighteenth tooth.....	123	128

Vertebræ.—Of the vertebral column of this specimen there are preserved the left neurapophysis of the atlas, four dorsal, two lumbar, and one sacral (second) vertebra. All of those present are of the procœlian type.

The neurapophysis, when compared with the homologous part in *Crocodylus americanus*, shows the anterior process to be a little longer and wider vertically, and the constriction above the articular end forming a somewhat deeper notch on the forward side.

The dorsals show the typical cup and ball articulation. The centra have the sides concave antero-posteriorly, with the least transverse diameter toward the posterior end. In all of the dorsals preserved the inferior surface is evenly rounded. In this respect they differ from those of *Leidyosuchus canadensis*, which are described as being flat in this aspect. The centra increase in breadth below the neuro-central suture. The neural arches inclose the neural canal which is slightly higher than wide. The arches of these vertebræ are firmly coossified with the centra, which furnishes additional evidence of the mature age of the individual. Two of the dorsal centra show shallow longitudinal depressions on the mid-lateral surfaces. None of the spinous processes are complete though the broken bases show them to have been broad antero-posteriorly. The transverse processes are given off well up on the sides of the arches. The most anterior dorsal, corresponding perhaps to the eighth in recent crocodiles, shows the same step-like facets with which the tubercula of the ribs articulate.

“a. Estimated.”

As Lambe has pointed out, the anterior zygapophyses together with the bases of the transverse processes form an undulating platform of considerable extent. The more nearly horizontal position of these zygapophyses would appear to distinguish the vertebræ from those of *L. canadensis*.

Measurements of dorsal vertebræ of *Leidyosuchus sternbergii*.

	I.	II.	III.	IV.
	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>
Greatest length of centra	30	30	33	34
Greatest transverse diameter, anterior end	19	20	20	20
Greatest vertical diameter, anterior end	19	19	18.5	19
Greatest transverse diameter, posterior end	17	17	19	20
Greatest vertical diameter, posterior end	17	16	16	16
Greatest antero-posterior extent of left transverse	19	..	..	..
Greatest length of left transverse from median line	48	..	..	..

The two lumbar vertebræ are probably the third and fourth of the series. Their centra differ from the dorsals in being more broadly rounded inferiorly and having their least transverse diameter nearer the middle. The neural canal is more nearly circular, and the transverse processes are narrower and spring from the sides of the arch at a lower level than in the dorsals, thus leaving the anterior zygapophyses standing out alone and well above them. The spinous processes rise above the middle of the centrum as a broad, thin plate with a truncated upper extremity (see *a*, fig. 1).

Measurements of lumbar vertebræ of *Leidyosuchus sternbergii*.

	Third.	Fourth.
	<i>mm.</i>	<i>mm.</i>
Greatest length of centra	30	30
Greatest transverse diameter, anterior end	20.5	21
Greatest vertical diameter, anterior end	18.5	18
Greatest transverse diameter, posterior end	20	20
Greatest vertical diameter, posterior end	16.5	17
Greatest antero-posterior extent of transverse	13	9.5
Greatest length of right transverse process from median line		37
Greatest width (antero-posteriorly) spinous process near top		20
Greatest width between outer edges of prezygapophyses		35

The concave, convex, articulating ends of the second sacral are much less pronounced than in the presacrals described above. The inferior surface is broad and only slightly rounded; the sacral ribs are heavy and firmly ankylosed with the whole side of the centrum and half way up on the neural arch. In size and general shape it

agrees in all essentials with the sacral figured by Lambe, . . . except in this species the neural canal is circular instead of being elongated vertically as in *Leidyosuchus canadensis* (See *b*, fig. 1.)

Measurements of second sacral vertebra of Leidyosuchus sternbergii.

	<i>mm.</i>
Greatest length of centrum	27.5
Greatest transverse diameter, anterior end	16
Greatest transverse diameter, posterior end	17
Greatest transverse diameter from middle of centrum to end of sacral rib	41
Greatest width between outer edges of postzygapophyses	23

Limb and foot bones.—The few bones of the limbs found with the type skull show that the proportional lengths of the fore and hind limbs in *Leidyosuchus* are approximately the same as in modern crocodiles, although the humeri, when compared with those of a specimen of *Crocodylus americanus* of the same size, are relatively more slender.

The general characteristics of these bones are well shown in fig. 2 and their principal dimensions are given in the table of measurements below.

Measurement of limb and foot bones of Leidyosuchus sternbergii.

	<i>mm.</i>
Greatest length of right humerus	164
Greatest width of proximal end of humerus	34
Greatest length of fibula	140
Greatest width of proximal end of fibula	27
Greatest width of distal end of fibula	25
Greatest length of metatarsal	84
Greatest width of proximal end of metatarsal	20
Greatest width of distal end of metatarsal	10

Scutes.—There were no scutes found with the holotype of *L. sternbergii*, but in a small collection of fossils made by Mr. A. L. Beekly from the Ceratops Beds (or their equivalent) on the Standing Rock Indian Reservation of South Dakota, were two dermal scutes (Cat. No. 6545, U. S. N. M.) of a crocodilian, which correspond closely in all respects to those figured by Lambe. These were associated with detached teeth which cannot be distinguished from those of *Leidyosuchus*, and the range of this genus is thus extended into South Dakota. These remains were associated with a typical Ceratops Beds fauna, the following forms having been recognized. *Triceratops*, *Trachodon*, *Champsosaurus*, *Basilemys*, and *Lepidosteus*."

The species may be considered valid.

DEINOSUCHUS Holland

ORIGINAL TYPE REFERENCE.—HOLLAND, W. J., 1909, 'Deinosuchus hatcheri, a New Genus and Species of Crocodile from the Judith River Beds of Montana,' Ann. Carn. Mus., VI, No. 1, Art. 4, p. 282.

SUBSEQUENT REFERENCE.—GILMORE, C. W., 1910, 'Leidyosuchus sternbergii, a New Species of Crocodile from the Ceratops Beds of Wyoming,' *Proc. U. S. Nat. Mus.*, XXXVIII, p. 501 (Pub. No. 1762).

TYPE.—*Deinosuchus hatcheri* Holland.

ORIGINAL TYPE DESCRIPTION.—“Great size, exceeding that of any other representative of the Crocodilia thus far described from North America. . . . Scutes massive and possessing great vertical height in comparison with their breadth, many of the smaller scutes being almost hemispherical, and some of the smallest subglobose. Pubis straighter and less deeply excavated posteriorly than in recent crocodilia. Extremities of spines of dorsal vertebræ broad transversely and thickened for attachments, much more so than in existing genera. The postzygapophyses of the vertebræ more nearly on the same plane as the transverse processes and not looking outwardly as much as in other crocodiles.”

The genus may be considered valid.

***Deinosuchus hatcheri* Holland**

ORIGINAL TYPE REFERENCE.—HOLLAND, W. J., 1909, 'Deinosuchus hatcheri, a New Genus and Species of Crocodile from the Judith River Beds of Montana,' *Ann. Carn. Mus.*, VI, No. 1, Art. 4, pp. 281–294, 16 figs.

SUBSEQUENT REFERENCES.—No subsequent references are available at the present time.

ORIGINAL TYPE FIGURES.—HOLLAND, W. J., 1909, 'Deinosuchus hatcheri, a New Genus and Species of Crocodile from the Judith River Beds of Montana,' *Ann. Carn. Mus.*, VI, No. 1, Art. 4, pp. 281–294, figs. 1–7, 9–16.

TYPE.—Two vertebræ, a cervical rib, one complete dorsal rib and fragments of others, a pubic bone and twenty-five scutes. *Carn. Mus.* No. 963.

TYPE LOCALITY AND LEVEL.—Willow Creek, three miles west of Nolan and Archer's ranch, Fergus County, Montana. Judith River Beds of Upper Cretaceous age.

ORIGINAL TYPE DESCRIPTION.—

“*Generic characters of Deinosuchus so far as known.* Great size, exceeding that of any other representative of the Crocodilia thus far described from North America.⁴ Scutes massive and possessing great vertical height in comparison with their breadth, many of the smaller scutes being almost hemispherical, and some of the smallest subglobose. Pubis straighter and less deeply excavated posteriorly than in recent crocodilia. Extremities of dorsal spines of vertebræ broad transversely and thickened for attachments, much more so than in existing genera. The postzygapophyses of the vertebræ more nearly on the same plane as the transverse processes and not looking outwardly as much as in other crocodiles.

Seventh (?) Dorsal Vertebra.

(C. M. Cat. Vert. Foss., No. $\frac{963}{1}$.)

The specimen, which almost beyond a doubt is the seventh in the dorsal series, is the better preserved of the two vertebræ which were recovered. It is procœlous. At the extremities of the transverse processes it shows the articulating surfaces for

⁴“The writer has carefully examined and inquired in various museums at home and abroad and has been unable to find in any of them the fossil remains of any crocodile from North America equaling in size those here reported upon.”

the ribs. It is a very massive bone and the dorsal spine is broad above, being greatly thickened transversely for attachment to adjacent structures. The postzygapophyses do not look as strongly outwardly as in the recent crocodilia, the under surfaces lying at their outer extremities nearly in the same plane as the upper surface of the transverse processes. Three views of the vertebra are given in Figures 1-3.

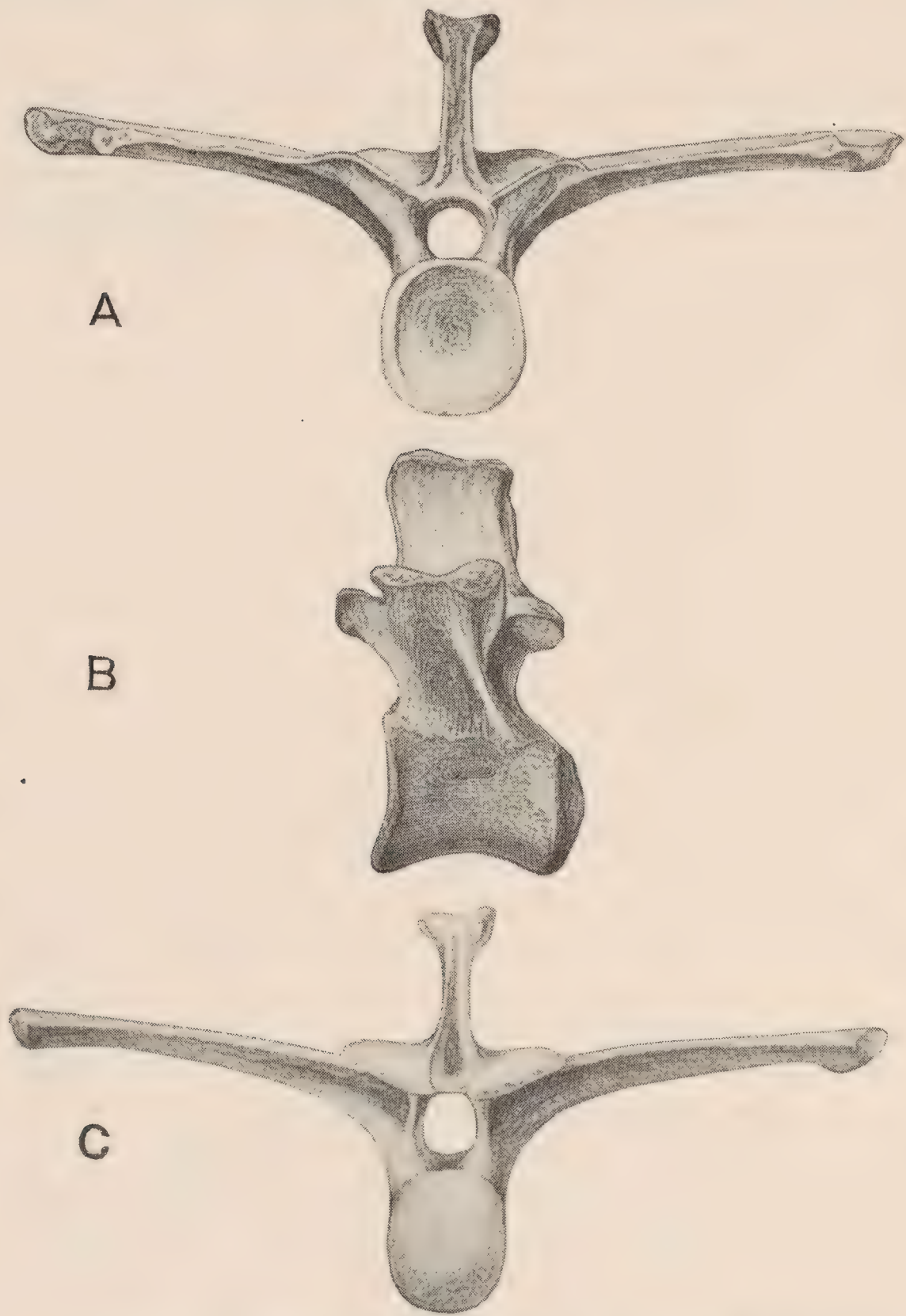


Fig. 53. *Deinosuchus hatcheri* Holland. Type specimen, seventh (?) dorsal vertebra (Carn. Mus. No. $\frac{963}{1}$). One-ninth natural size. A, anterior view; B, lateral view, left side; C, posterior view. Original type figures. (After Holland.)

DIMENSIONS.

Extreme width from tip to tip of transverse processes	680 mm.
Height from bottom of centrum to tip of spine	310 “
Extreme length across zygapophyses	180 “
Length of centrum at middle	140 “
Length of centrum along floor of neural canal	125 “

DIMENSIONS (*Continued*)

Vertical diameter of centrum in front	122	"
Transverse diameter of centrum in front	122	"
Vertical diameter of centrum behind	110	"
Transverse diameter of centrum behind	95	"
Vertical diameter of neural canal	52	"
Transverse diameter of neural canal	35	"
Height of spine above neural canal	150	"
Height of spine above postzygapophyses	105	"
Height of spine above prezygapophyses	135	"
Antero-posterior diameter of spine at base	110	"
Antero-posterior diameter of spine at top	87	"
Transverse diameter of spine at base posteriorly	30	"
Transverse diameter of spine at base anteriorly	30	"
Transverse diameter of spine at top	65	"
Distance across postzygapophyses	173	"
Distance across prezygapophyses at their base	230	"

LAST LUMBAR VERTEBRA

(C. M. Cat. Vert. Foss., No. $\frac{963}{2}$.)

The vertebra under consideration is not so well preserved as the one described in the preceding paragraph, but the extremity of the left transverse process is sufficiently complete to show that it did not carry ribs. I assign it with doubt to the position of the last member of the lumbar series on account of the manner in which the spine and postzygapophyses overhang backwardly. If not that it must be one or the other of the two vertebræ immediately preceding. In general appearance it is not unlike the seventh (?) vertebra already described, except that the transverse processes are much narrower and the left, which is well preserved, shows no articular surfaces at the end. The spine has a much smaller antero-posterior diameter at the top than the seventh dorsal and its posterior margin is placed more decidedly caudad than in that vertebra. Fig. 4 shows the left side of the vertebra, which is the more complete, which may be compared with the corresponding view of the seventh dorsal.

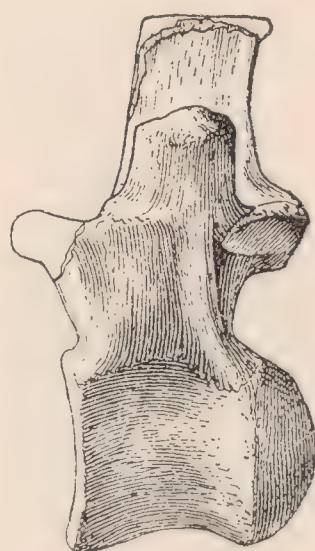


Fig. 54. *Deinosuchus hatcheri* Holland. Type specimen, last (?) lumbar vertebra (Carn. Mus. No. $\frac{963}{2}$).

One-ninth natural size. Lateral view, left side. Original type figure. (After Holland.)

DIMENSIONS

Extreme width from tip to tip of transverse processes*	670 (?) mm.
Height from bottom of centrum to tip of spine†	320± "
Extreme length across zygapophyses	160± "
Length of centrum at middle	150 "
Length of centrum along floor of neural canal	90 "

*The right transverse process is broken; the measurement given represents twice the distance from the middle of the spine to the end of the left transverse process."

†The top of the spine appears to be broken, and may not quite represent the true length in life."

DIMENSIONS (*Continued*)

Vertical diameter of centrum in front	130	"
Transverse diameter of centrum in front	105	"
Vertical diameter of centrum behind	110	"
Transverse diameter of centrum behind	85	"
Vertical diameter of neural canal	53	"
Transverse diameter of neural canal	35	"
Height of spine above neural canal	158±	"
Height of spine above postzygapophyses	105	"
Height of spine above prezygapophyses	155	"
Antero-posterior diameter of spine at base	110	"
Antero-posterior diameter of spine at top	67	"
Transverse diameter of spine at base posteriorly	28	"
Transverse diameter of spine at base anteriorly	10	"
Transverse diameter of spine at top	40±	"
Distance across postzygapophyses	200	"
Distance across prezygapophyses at their base	230±	"

CERVICAL RIB

(C. M. Vert. Cat. Foss., No. $\frac{963}{3}$.)

A fairly well preserved specimen of the first cervical rib of the left side was found. At its proximal end it has been somewhat broken, but not enough to greatly diminish its length. Its proportions and general appearance are represented in Fig. 5, *a* representing the inner, and *b* the outer surface of the bone.

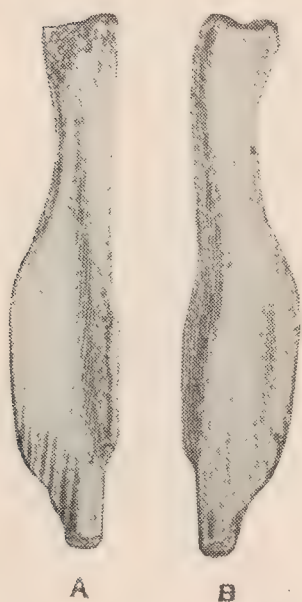


Fig. 55. *Deinosuchus hatcheri* Holland. Type specimen, left first cervical rib (Carn. Mus. No. $\frac{963}{3}$).

One-sixth natural size. A, internal view; B, external view. Original type figures. (After Holland.)

DIMENSIONS

Greatest length	235 mm.
Width at proximal end	37 "
Smallest width at proximal end	28 "
Greatest width in distal half	51 "
Width at distal extremity	17 "
Transverse diameter at proximal end	18 "
Transverse diameter at distal end	8 "

DORSAL RIBS

(C. M. Cat. Vert. Foss., No. $\frac{963}{4}$.)

A fairly well preserved specimen of the first dorsal or thoracic rib of the left side was recovered. Its shape is represented in Fig. 6, *A* showing the posterior, and *B* the anterior surface of the rib. It had been broken about the middle of the shaft

and was repaired in the laboratory. The writer has been assured that the contacts within, which are not now visible, justified the proportions which are shown by the specimen, but nevertheless, is disposed to believe that the restored bone does not quite fully represent the entire length of the sternal part as it was in life. It is proportionately considerably shorter in its total length than the corresponding bone in other crocodilians. The relative length and shape of the capitulum and tuberculum is very like what is seen in the crocodiles of to-day. The tuberosity is well developed and directed forward and slightly more downward than in recent crocodilia.

In addition to the specimen which is here figured there were found a number of fragments of ribs, one of them apparently the proximal end with the capitulum of the third thoracic rib of the left side; another evidently a piece of the upper portion of the first rib of the right side carrying the tuberosity, but lacking the capitulum and tuberculum, and still another which is apparently the proximal end of the fifth dorsal. A few fragments of the distal end of the ribs also occur in the mass of bones picked up by Mr. Utterback.

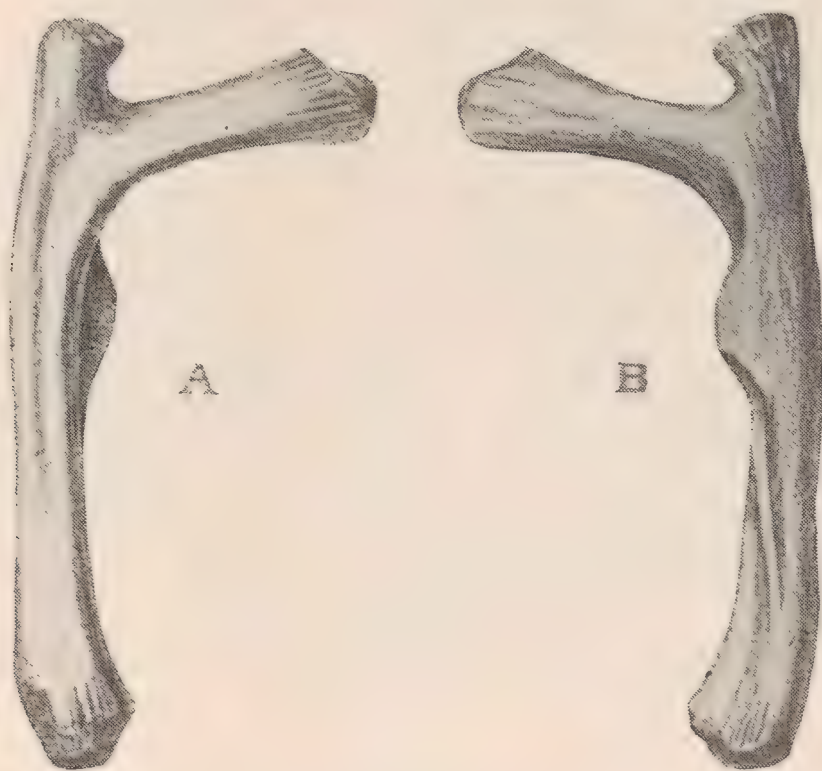


Fig. 56. *Deinonychus hatcheri* Holland.
Type specimen, left first dorsal rib (Carn.
Mus. No. $\frac{963}{4}$).

One-eighth natural size. A, posterior view; B,
anterior view. Original type figure. (After Holland.)

DIMENSIONS

(First left dorsal rib. See Fig. 6.)

Greatest length from end of tuberculum to distal extremity	460 mm.
Distance from outer edge of tuberculum to extremity or capitulum	220 "
Greatest width of rib over tuberosity	80 "
Greatest width of capitulum at end	60 "
Antero-posterior diameter of capitulum at end	32 "
Greatest width of tuberculum at end	50 "
Antero-posterior diameter of tuberculum	30 "
Greatest width of distal end of rib	60 "
Antero-posterior diameter of rib at end	35 "

THE PUBIS

(C. M. Cat. Vert. Foss., No. $\frac{963}{11}$.)

A very well preserved specimen of the right pubic bone was recovered. It agrees very closely in its general outline and proportions with the corresponding bone in recent crocodiles, but is somewhat less rounded on its distal margin and decidedly less excavated on its posterior margin, at least when compared with the specimens of *Crocodylus* and *Alligator* before me. It is represented in Fig. 7, the illustration at the

left of the cut showing the superior, and that on the right of the cut the inferior surfaces of the bone, the strongly curved, or excavated, side being the anterior margin.

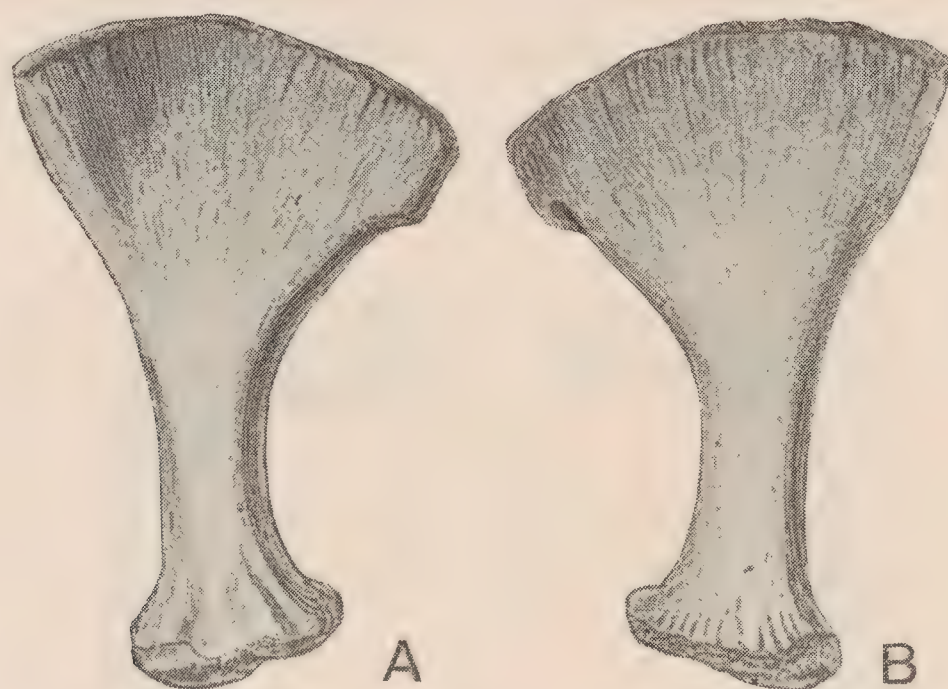


Fig. 57. *Deinonychus hatcheri* Holland.
Type specimen, right pubis (Carn. Mus. No. $\frac{963}{11}$).

One-sixth natural size. A, superior view; B, inferior view. Original type figure. (After Holland.)

DIMENSIONS

Distance from proximal extremity to distal extremity of posterior margin	287 mm.
Distance from proximal extremity to distal extremity of anterior margin	223 "
Antero-posterior diameter of proximal end	100 "
Vertical diameter of proximal end	55 "
Smallest antero-posterior diameter of shaft	45 "
Vertical diameter of shaft	30 "
Greatest width of distal end	200 "
Vertical diameter at posterior angle of distal margin	23 "
Vertical diameter at anterior angle of distal margin	10 "

THE SCUTES.

Of the scutes representing the specimen there are twenty-five, which are in fairly good condition, and numerous fragments of others.

In a beautifully perfect skeleton of *Crocodylus acutus floridanus* before me as I write I find that there are ninety-two osseous scutes entering into the dermal covering of the neck and back. The anterior series forms a transverse row of four scutes located immediately over and covering the spine of the axis; the second series consists of two transverse rows, the first made up of four scutes, the second of two scutes, and these overlie and cover the spines of the third, fourth, and fifth cervicals. The third series is composed of two scutes, covering the spine of the sixth cervical. The spine of the seventh cervical is not shielded above by a row of scutes; and the spine of the eighth cervical is only partially covered by the first transverse row of the dorsal series of scutes. The dorsal series is made up of fifteen transverse rows of scutes, each row composed of four or six bony plates. Those containing six plates are the second,

the fifth, the eighth, the tenth, eleventh, and twelfth rows, reckoning backward. The fifteenth transverse row of scutes, overlies and covers the spines of the third and fourth lumbar vertebræ. Following the dorsal series of scutes terminating at the point just stated, there are on either side, extending backward over the region of the sacrum



Fig. 58. *Deinonychus hatcheri* Holland. Type specimen, cervical scute (Carn. Mus. No. $\frac{963}{12}$).

One-half natural size. A, superior view; B, inferior view. Original type figures. (After Holland.)

and the two anterior caudal vertebræ, six bony scutes diminishing in size backward and forming the backward prolongation of the second longitudinal row of scutes reckoning from the median line outwardly on either side. The arrangement of the scutes in *C. floridanus* is represented diagrammatically in Fig. 8.

All the scutes in *D. hatcheri* are characterized on the superior surface by an elevated longitudinal median ridge or carina, which does not, however, rise as sharply

from the surface as in recent genera, and as is shown in the figures herewith given, passes by almost insensible degrees into the surface of the adjoining parts of the scutes.

An attempt has been made by comparison with the scutes as they exist upon the back of recent crocodiles to ascertain the relative position of the scutes belonging to the specimen of *Deinosuchus hatcheri*, but the result has not been wholly satisfactory to the writer. The scute represented in Figs. 9 and 10 appears to undoubtedly correspond to the internal right scute of the first row in the second cervical series, and the scute represented in Figs. 11-13 to be its immediate successor in the second row of the same series. Fig. 14 represents what the writer believes to be the left scute of the third cervical series. The smaller scute represented in Fig. 16 no doubt belongs to the sacro-caudal series, and the large broad scutes, of which there are several well-preserved specimens, one of them shown in Fig. 15, can be referred approximately to their places about the middle of the dorsal series.



Fig. 59. *Deinosuchus hatcheri* Holland. Type specimen, cervical scute (Carn. Mus. No. $\frac{963}{13}$).

About one-fourth natural size. A, dorsal view; B, posterior view; C, lateral view, right side; *a*, anterior margin; *b*, posterior margin; *l*, left side; *r*, right side. Original type figures. (After Holland.)

The scutes differ from those of all other crocodilia by their great vertical thickness in comparison with their length and breadth. They are not proportionally nearly as thin as those of any recent species, and the writer cannot discover in the literature of the subject, nor has he found in any of the collections at home or abroad crocodilian scutes which are so heavy and massive as these. The smaller scutes are some of them almost hemispherical and a few of the smallest almost spherical in form, causing them thus to differ widely in appearance from those of other crocodilian scutes. This character is regarded by the writer as possessing generic value.

On the upper surface all of the scutes are deeply pitted on either side of the median longitudinal ridge, the pits being often confluent. The median ridge is also in almost all cases marked by a few narrow but deep circular pits. On the under side the scutes are slightly rounded at their edges in the case of the larger specimens, and quite rounded in the cases of the smaller specimens. They show on the under surface numerous fine straight lines decussating with each other at an angle of about forty-five degrees, indicating the structure of the dermal tissues in which they were imbedded and to which they adhered.* On the anterior margin many of the scutes show bevelled margins to adapt them to union with the scutes which preceded them and evidently somewhat overlapped them in front.

*Sir Richard Owen (Report of the British Association for the Advancement of Science, 11th meeting, 1841, p. 71) calls attention to a similar feature in the scutes of *Goniopholus crassidens* Owen."

DIMENSIONS OF SCUTES

Cervical Scute. (See Figs. 9 and 10.)

(Carnegie Museum Cat. Vert. Foss., No. $\frac{863}{12}$.)

Antero-posterior diameter	111 mm.
Transverse diameter	143 "
Greatest vertical diameter	58 "

? Cervical Scute (See Figs. 11-13.)

(Carnegie Museum Cat. Vert. Foss., No. $\frac{863}{13}$.) [963. ?]

Antero-posterior diameter	80 mm.
Transverse diameter	115 "
Greatest vertical diameter	60 "

Dorsal Scute (See Fig. 15.)

(Carnegie Museum Cat. Vert. Foss. No. $\frac{963}{14}$.)

Antero-posterior diameter	103 mm.
Transverse diameter	160 "
Greatest vertical diameter	42 "

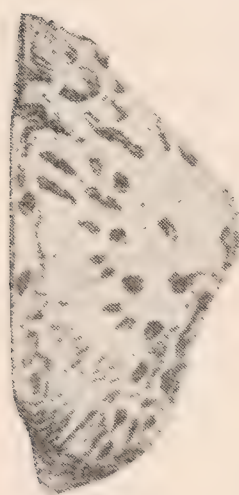


Fig. 60

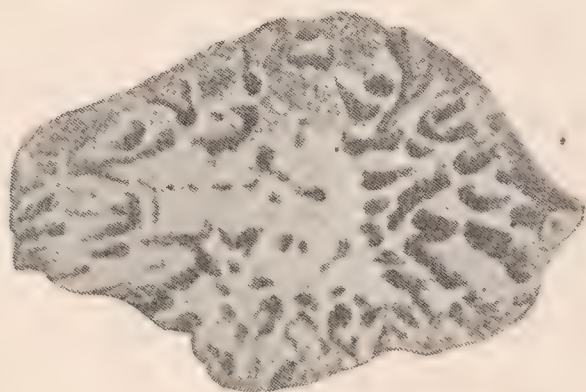


Fig. 61



Fig. 62

Fig. 60. *Deinosuchus hatcheri* Holland. Type specimen, cervical scute (Carn. Mus. No. $\frac{963}{15}$).

About one-fourth natural size. Anterior view. Original type figure. (After Holland.)

Fig. 61. *Deinosuchus hatcheri* Holland. Type specimen, dorsal scute (Carn. Mus. No. $\frac{963}{14}$).

About one-fourth natural size. Superior view. Original type figure. (After Holland.)

Fig. 62. *Deinosuchus hatcheri* Holland. Type specimen, sacro-caudal scute (Carn. Mus. No. $\frac{963}{16}$).

About one-fourth natural size. 1, superior view; 2, lateral view, left side; 3, posterior view; *a*, anterior margin; *b*, posterior margin. Original type figure. (After Holland.)

Sacro-caudal Scute (See Fig. 16.)

(Carnegie Museum Cat. Vert. Foss. No. $\frac{963}{16}$.)

Antero-posterior diameter	60 mm.
Transverse diameter	37 "
Greatest vertical diameter	33 "

COMPARATIVE MEASUREMENTS OF THE CORRESPONDING BONES IN THE SKELETON OF
CROCODYLUS FLORIDANUS (Carnegie Museum Accession No. $\frac{1010}{2}$) AND
THE TYPE OF DEINOSUCHUS HATCHERI
(Carnegie Museum Cat. Vert. Foss., No. 963).

Cervical Rib.

	<i>C. floridanus.</i>	<i>D. hatcheri.</i>
Length	105 mm.	235 mm.
Width at proximal end	12 "	37 "
Smallest width in proximal half	9 "	28 "
Greatest width in distal half	13 "	51 "
Width at distal end	5 "	17 "
Transverse diameter at proximal end	6 "	18 "
Transverse diameter at distal end	2.5 "	8 "

Dorsal Rib.

Greatest length from end of tuberculum to distal extremity	125 mm.	460 mm.
Distance from outer edge of tuberculum to end of capitulum	50 "	220 "
Greatest width of rib over tuberosity	22 "	80 "
Greatest width of capitulum at end	10 "	60 "
Greatest width of tuberculum at end	15 "	50 "
Greatest width of distal end of rib	13 "	[?] 60 "

Pubis.

Distance from proximal end to distal end of posterior margin	78 mm.	287 mm.
Distance from proximal end to distal end of anterior margin	80 "	223 "
Antero-posterior diameter of proximal end	23 "	100 "
Vertical diameter of proximal end	15 "	55 "
Smallest antero-posterior diameter of shaft	12 "	45 "
Vertical diameter of shaft	9 "	30 "
Greatest width at distal end	54 "	200 "
Vertical diameter at posterior angle of distal margin	5 "	23 "
Vertical diameter at anterior angle of distal margin	2.5 "	10 "

Seventh Dorsal Vertebra.

Extreme width across transverse processes	158 mm.	680 mm.
Height from bottom of centrum to top of spine	60 "	310 "
Length across zygapophyses	60 "	180 "

Last(?) Lumbar Vertebra.

Extreme width across transverse processes	135 mm.	670 mm.
Height from bottom of centrum to top of spine	83 "	320 "
Length across zygapophyses	58 "	160 "

The measurements given in the foregoing comparative table for *Crocodylus floridanus* yield a total of 1220, from which we obtain a general average of 43.5. The total of the measurements given for *Deinosuchus hatcheri* is 4617, yielding us a general

average of 164.8. The length of the specimen of *Crocodylus floridanus* from the tip of the nose to the end of the tail, from which the measurements in the first column were derived, is 3050 mm. In the ratio of 43.5 to 164.8 we would find that the total length of *Deinosuchus hatcheri*, provided it was built on the same relative proportions as *Crocodylus floridanus*, would be 13,830 mm., or about 45 feet in length.

This method of calculating may be open to objection and the result may be somewhat excessive. We may approach the problem in another way. We may assume that the length of the seventh dorsal vertebra represents the average length of the vertebræ in the series. In fact the centra of the caudals about the middle of the tail in all crocodilian skeletons I have examined considerably exceed in length the centra of the anterior vertebræ, though the last eight or nine rapidly decrease. The centrum of the seventh dorsal in the specimen of *C. floridanus* before me certainly is rather under than over the average length of the members of the series. The length of the seventh dorsal in *D. hatcheri* is almost exactly six inches. The number of vertebræ in the total series is sixty (?). This would give us a length of thirty feet, without taking into account the length of the skull from its point of union with the atlas to the tip of the snout, which in *C. floridanus* is as 13 to 60. Applying this proportion to the case in hand we would have a length of from five to six feet for the skull. Adding this to the length of the vertebral column back of the head we have thirty-five as the total length of the bony framework of the animal. It is therefore no exaggeration to say that *D. hatcheri* must have been a crocodile which possessed a length of from thirty-five to forty feet, exceeding thus in length the largest specimen of *C. porosus* of which we have record, which is said to have been thirty-three feet in length, and therefore the longest crocodile belonging to a living species, which has ever been observed.

Deinosuchus hatcheri was undoubtedly one of the hugest representatives of the Crocodilia which has existed upon our globe."

The species may be considered valid.

BRACHYCHAMPSA Gilmore

ORIGINAL TYPE REFERENCE.—GILMORE, C. W., 1911, 'A New Fossil Alligator from the Hell Creek Beds of Montana,' Proc. U. S. Nat. Mus., XLI, pp. 297-302 (Pub. No. 1860).

SUBSEQUENT REFERENCE.—MEHL, M. G., 1916, 'Caimanoidea visheri, a New Crocodilian from the Oligocene of South Dakota,' Journ. Geol., XXIV, p. 50.

TYPE.—*Brachychampsia montana* Gilmore.

ORIGINAL TYPE DESCRIPTION.—The characters of the genus were not separated from those of the type species by Gilmore. See *Brachychampsia montana*.

The genus may be considered valid.

Brachychampsia montana Gilmore

ORIGINAL TYPE REFERENCE.—GILMORE, C. W., 1911, 'A New Fossil Alligator from the Hell Creek Beds of Montana,' Proc. U. S. Nat. Mus., XLI, pp. 297-302, 1 fig., Pls. XXVI, XXVII (Pub. No. 1860).

SUBSEQUENT REFERENCE.—MEHL, M. G., 1916, 'Caimanoidea visheri, a New Crocodilian from the Oligocene of South Dakota,' Journ. Geol., XXIV, p. 50.

ORIGINAL TYPE FIGURES.—GILMORE, C. W., 1911, 'A New Fossil Alligator from the Hell Creek Beds of Montana,' Proc. U. S. Nat. Mus., XLI, pp. 297-302, fig. 1, Pls. xxvi, xxvii (Pub. No. 1860).



Fig. 63. *Brachychampsia montana* Gilmore. Type specimen, twelfth maxillary tooth (Amer. Mus. No. 5032).

Natural size. *a*, lateral view; *b*, posterior view. Original type figure. (After Gilmore.)

TYPE.—The anterior two-thirds of the skull, accompanied by detached fragments of the posterior portion. Amer. Mus. No. 5032.

TYPE LOCALITY AND LEVEL.—Twenty-five miles south-east of Lismas, Dawson County, Montana. Hell Creek Beds. Upper sandstone.

ORIGINAL TYPE DESCRIPTION.—“The type-specimen is a short, broad-snouted skull, the length from the level of the front border of the orbits being only 7 mm. greater than the width at the same point. Excepting a few detached fragments, the posterior portion of the skull behind the orbits is missing (Pl. 26). The remaining part is fairly complete and undistorted. The upper surface of the preorbital region is flat and without crests or ridges; the muzzle is evenly but broadly rounded; the nasal aperture is large and pear-shaped in outline. In the absence of a roof-like covering formed by the premaxillaries over the anterior part of the external nares, *Brachychampsia* differs from all known alligators, both recent and extinct. On account of the damaged condition of the anterior extremities of the nasal bones it can not be determined whether they extended forward into the narial opening. The facial processes of the premaxillaries extend posteriorly to the level of the alveolus for the fifth maxillary tooth. The nasal bones are comparatively slender and extend posteriorly to the level of the anterior borders of the orbits. In recent alligators these bones terminate well in front of the orbital line. The maxillaries are broad, flattened above, and much compressed vertically. The jugals are heavy, with roughly sculptured surfaces. The interorbital surface is flat and not concave as in many crocodiles and alligators. The orbital openings are everted as in the alligators and some crocodiles and are confluent with the lateral vacuities. The sculpturing of the facial surface of the bones is more strongly marked in the neighborhood of the orbits than it is anteriorly.

In the palatal view (Pl. 27), where the bones have not suffered mutilation, all of the sutures are plainly indicated. Latero-inferiorly the maxillo-premaxillary suture passes obliquely backward and inward on the palate. The damaged condition of the palate just back of the anterior palatine vacuity renders uncertain the posterior extent of the premaxillaries. In the recent alligators this suture extends nearly straight across on a level with the second maxillary tooth, while in this form it extends posteriorly at least as far as the level of the fourth maxillary tooth.

Each of the broad maxillaries has alveoli for 14 teeth, and each of the premaxillaries for 5. The palatines, of which only the anterior portions are present, unite with the maxillæ by an almost straight transverse suture on a level with the eleventh maxillary tooth. The lateral borders of the anterior ends of the palatines are divergent, as in all alligators, instead of parallel or convergent as in all true crocodiles. On the left side of the palate enough of the boundary of the posterior palatine vacuity remains to indicate that it was subround instead of elongate as in most members of this group. The preserved borders of the anterior palatine vacuity show it to have been of large size and probably pear-shaped in outline.

The pits on the palatal surface of the premaxillary for the reception of the anterior teeth of the lower jaw are broad and exceedingly shallow.

A detailed fragment of the pterygoid shows the processes to have been blunt and stout.

Measurements of skull of Brachychampsa montana. Type specimen.

	mm.
Distance from anterior angle of orbits to tip of snout	164
Width of skull at anterior angle of the orbits.....	157
Width of skull at maxillo-premaxillary suture.....	105
Greatest width of nasal opening.....	44
Greatest longitudinal length of premaxillary.....	80
Least width of interorbital bar.....	26
Greatest width of nasals.....	32
Greatest width of anterior palatine processes.....	45
Greatest width of anterior palatine vacuity.....	33
Distance from anterior end of palatine vacuity to tip of snout.....	24
Length of alveolar border of maxillary.....	135
Length of alveolar border of premaxillary.....	65

Teeth —The dental formula of the upper jaw consists of 5 premaxillary and 14 maxillary teeth, the total number (38) being the same as found in the upper mandible of many modern alligators. Judging from the size of the alveoli, all of the premaxillary teeth appear to have been of approximately the same size. The teeth still present in the skull are: the bases of three premaxillary teeth, and the third, fourth, fifth, sixth, seventh, ninth, eleventh, and twelfth maxillary teeth on the right side; the roots of the third, fifth, sixth, and seventh, with the tenth and eleventh teeth intact, in the left maxillary. The first three maxillary teeth were relatively small and evidently of about equal size. The fourth is slightly larger than the third; the fifth is larger than the fourth and is the most robust tooth of the anterior dental series; the sixth tooth is slightly smaller than the fifth; the seventh, eighth, ninth, and tenth were quite small, being the weakest of those in the upper mandible; the eleventh and twelfth were robust, and, judging from the size of the alveoli for the thirteenth and fourteenth, all of these teeth were of approximately the same size.

The anterior teeth of the maxillary series although somewhat compressed transversely are acutely pointed, and while the fifth is as long as the eleventh and twelfth the anterior posterior extent of the tooth is only a little over half that of the latter. The relative dimensions are well shown in the table of measurements of the teeth given below.

The posterior teeth of *Brachychampsa montana* resemble most nearly those figured by Leidy. . . as *Bottosaurus harlani* from the Cretaceous of New Jersey. . . .

The crowns of the posterior teeth are somewhat compressed laterally, mammili-form, with outer and inner surfaces separated by a somewhat obscure carinæ which extends from the subacute apex to the base of the corrugated surface as shown in figure 1. The upper surface is corrugated with depressions radiating from the apex but the base of the enameled surface is smooth. The upper part of the tooth is separated from the gibbous root by a slight constriction at the base of the enamel.

In the collection of the U. S. National Museum there is a large number of detached teeth from the 'Ceratops beds' of Converse County, Wyoming, which can

not be distinguished from those in the specimen under discussion. With them are other teeth, which from their minute size and other differences appear to indicate the presence in those beds of one or more undescribed species, but the material is too meager upon which to base a determination. Many of these scattered teeth showed wear on their internal surfaces, thus substantiating the evidence of the *Alligatoroid* nature of the bite as shown by the worn posterior teeth of the type-specimen.

Principal measurements of maxillary teeth of Brachychampsia montana. Type-specimen.

Number of tooth.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Length.....	9	10	12	9	7	5	6.5	12	11
Extent antero- posteriorly.....	6.5	7	8	7	6	5	6	12	12"

The species is valid beyond all question of doubt.

PLATES IV AND V

PLATE IV

Brachychampsia montana Gilmore

Type specimen, anterior portion of skull

Amer. Mus. No. 5032

Natural size

Superior view

e. na., external nares; *fr.*, frontal; *ju.*, jugal; *mx.*, maxillary; *n*, nasal; *o.*, orbit; *p. mx.*, premaxillary.

Original type figure. (After Gilmore.)

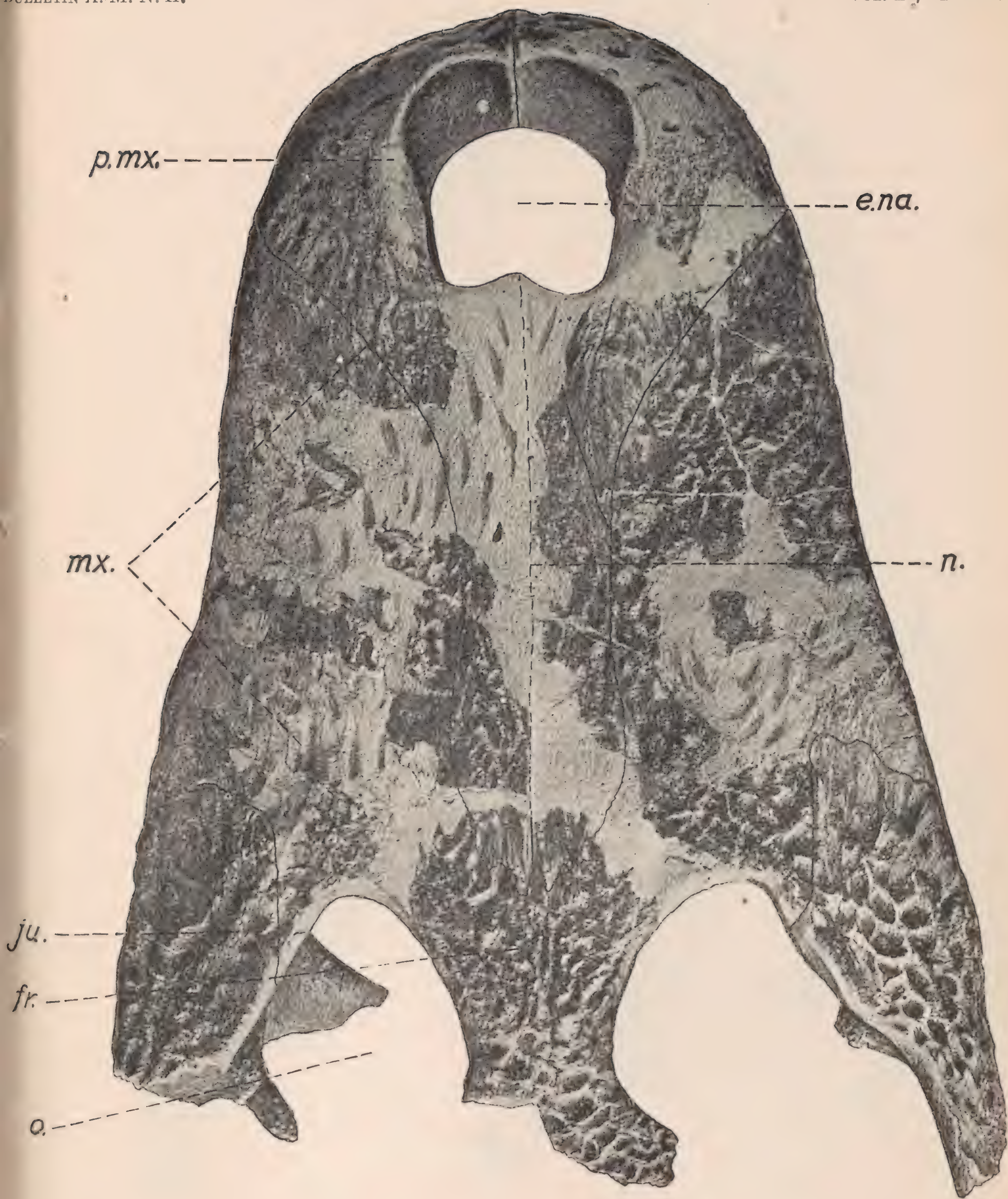


PLATE V

Brachychampsia montana Gilmore

Type specimen, anterior portion of skull

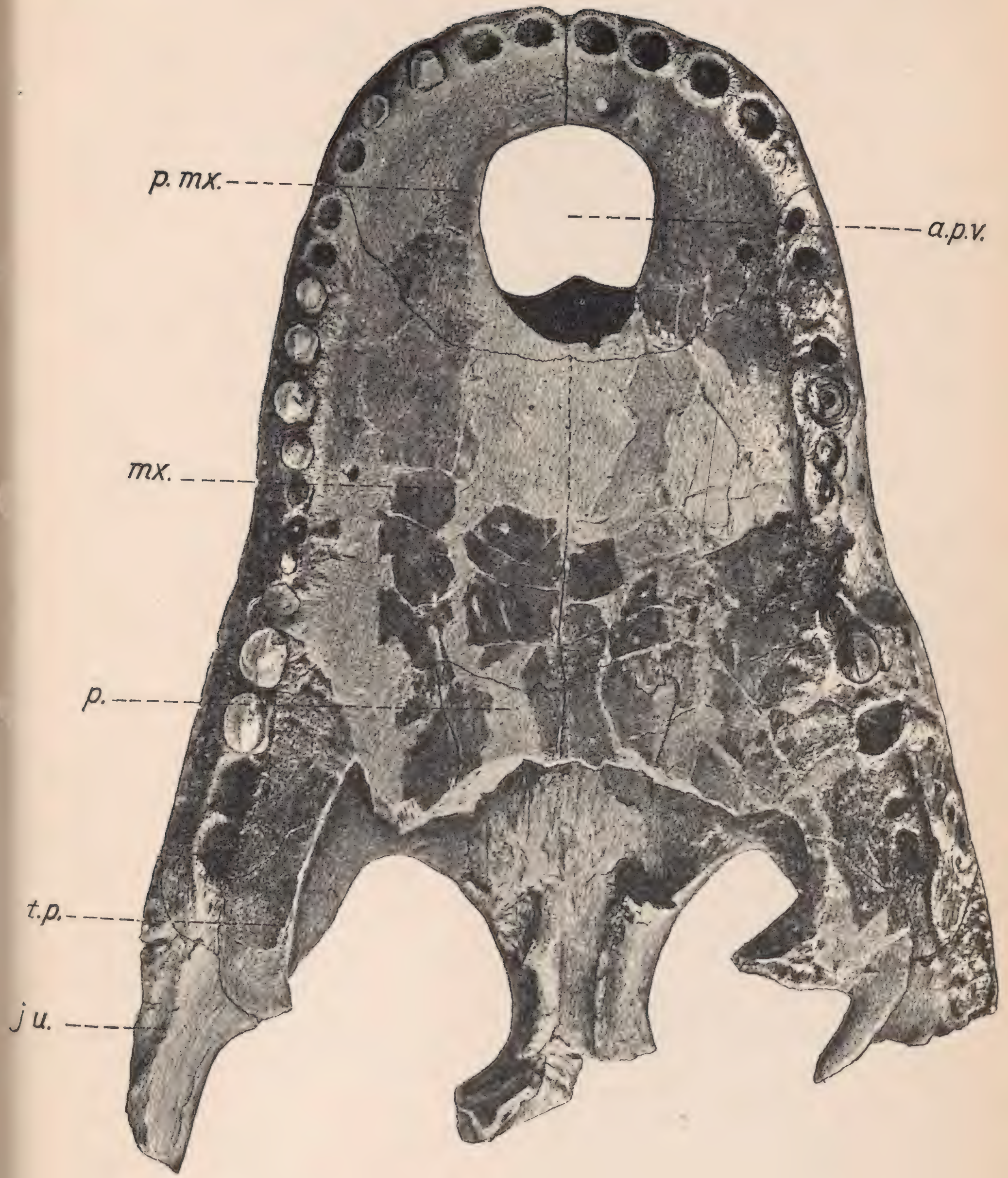
Amer. Mus. No. 5032

Natural size

Inferior view

a.p.v., premaxillary foramen; *ju.*, jugal; *mx.*, maxillary; *p.*, palatines; *p.mx.*, premaxillary; *t.p.*, ectopterygoid (transpalatine)

Original type figure. (After Gilmore.)



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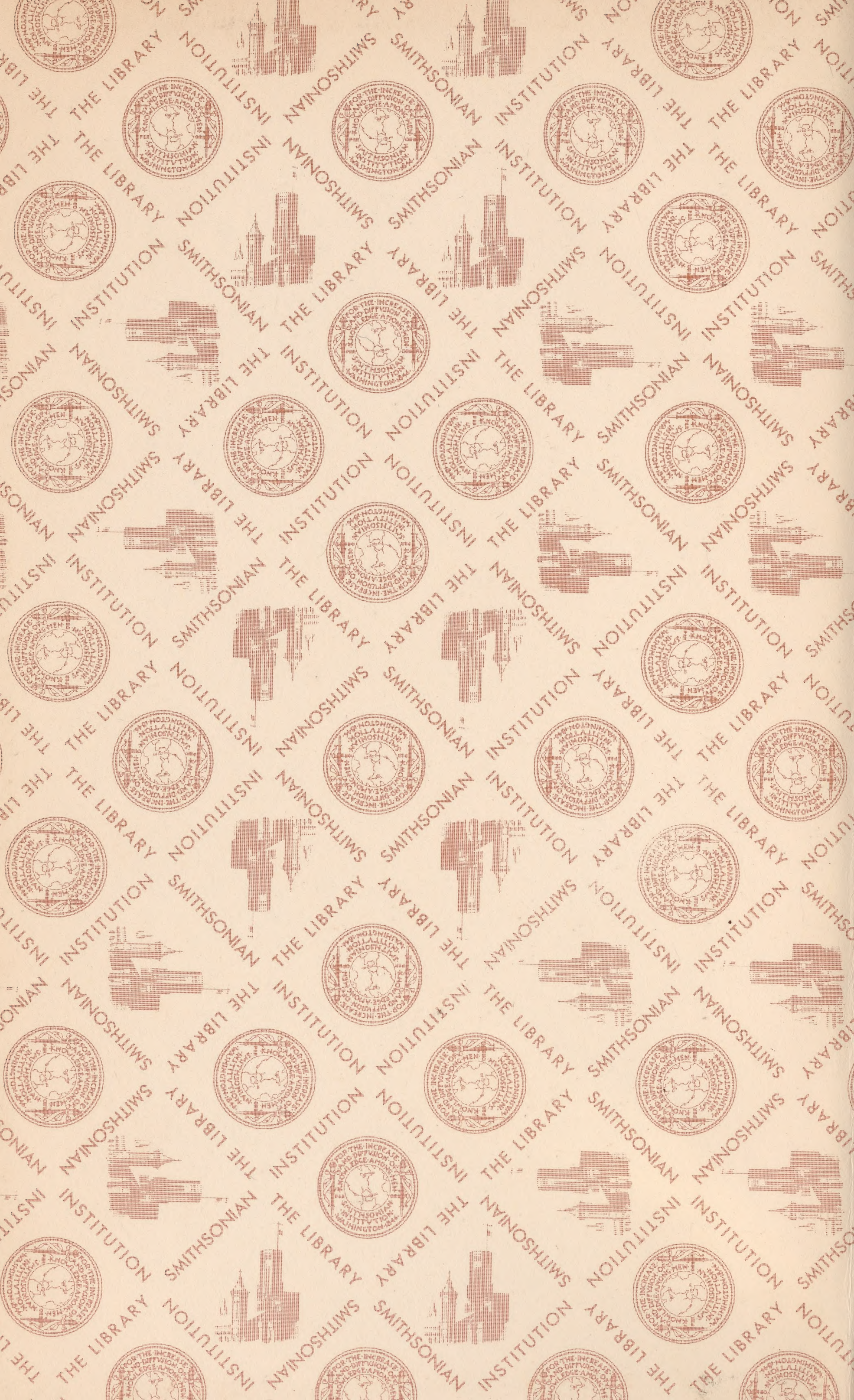
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